MANUAL OF METHODS FOR FISH STOCK ASSESSMENT

PART 1. FISH POPULATION ANALYSIS

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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Manual of sampling and statistical methods for fisheries biology. Part 2. Statistical methods. Section 6 *et seq.*

Manual of methods for fish stock assessment. Part 5. Direct assessment.

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MANUAL OF METHODS FOR FISH STOCK ASSESSMENT

PART 1. FISH POPULATION ANALYSIS

by

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME 1969

NOTE

Preliminary English versions of this manual have been issued as FAO Fisheries Technical Papers FIb/40, 1964; FIb/40 (Rev. 1), 1965; FRs/40 (Rev. 2), 1968. They have been based on, or used as lecture notes at various training centres as follows:

U.S. Fish and Wildlife Service	(Beaufort, North Carolina)	1951
International Council for the Exploration of the Sea	(Lowestoft, United Kingdom)	1957
FAO/EPTA	(Bangkok, Thailand)	1958
Commonwealth Scientific and Industrial Research Organization	(Cronulla, Australia)	1962
International Council for the Exploration of the Sea	(Lowestoft, United Kingdom)	1963
FAO/EPTA	(Cronulla, Australia)	1964
FAO/EPTA	(Viña del Mar, Chile)	1966
FAO/UNDP	(Copenhagen, Denmark)	1968

The various revisions of the manual have been based to a large extent on the discussions and experiences of these training centres. Over this period contributions to these notes have been made by E.L. Cadima (who drafted the subsection on mathematics), R.J.H. Beverton, R. Jones, B.B. Parrish, K.P. Andersen, S.J. Holt, L.K. Boerema and others.

A French translation of a preliminary version, *Méthodes d'analyse des populations de poissons*, translated by F. Baudin-Laurencin and others, was issued by the Office de la recherche scientifique et technique outremer, Pointe-Noire, Congo in 1965. *Métodos de análisis de poblaciones de peces*, a Spanish translation by R. Coyula, N. Cruz and E.L. Cadima, was issued by the Centro de Investigaciones Pesqueras, Cuba, in 1966. These translations included certain amendments and revisions, which have been included in this final version.

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SECTION 1. INTRODUCTION

In studying the state of the fish stocks and the effect of fishing on them, the fishery biologist should carry out his analysis in precise quantitative terms. To do this he must use mathematics, and to use mathematics the complexities of the real situation must be replaced by more or less simplified and abstract mathematical models. Such models may be used to represent both quantities of interest (abundance of the population, size of the individual fish), and the relation between these quantities.

In their simplest form, mathematical models are regularly used by biologists; for instance, it is commonplace to represent the size of a fish by the number of centimetres between the tip of its jaw and the end of its caudal fin. This model conceals many factors about the actual fish — whether it is fat or thin, or whether it is a cod or a tuna — but enables many analyses to be carried out — e.g. the construction of a length-frequency distribution of a sample of the fish population.

The value of a model may be judged by its simplicity and the closeness with which events or values predicted by the model fit the actual observation. A model cannot be considered as being either right or wrong, but as giving a satisfactory fit to the facts over a wide or narrow range of situations. A good model is one that is simple, but gives a good fit over a wide range.

The best test of a model is its usefulness in prediction; in this sense prediction covers not only the prediction of future events but also any values or events not considered in proposing the model. Thus a model describing the growth of cod in length may be proposed from the analysis of data of mean length at age; it will be a more useful model if, subject to the fitting of a minimum number of constants, it can be used to predict (estimate) the mean length at age of haddock, or any other species.

All the models described in this manual have proved to a greater or lesser extent to be useful models in that they have provided useful quantitative descriptions of events in various fisheries. Most have also been successful in making predictions, in the sense used above. A good example of the testing of a model by a successful prediction is the analysis of the Antarctic whale stocks. At the 1963 meeting of the International Whaling Commission there was considerable discussion on the

quota, in terms of numbers of whales caught, to be set for the 1963/64 season. The Commission's Committee of Three Scientists had devised a model for the population of Antarctic fin whales, taking into account the probable rates of mortality and recruitment, etc. On the basis of this model the Committee had recommended that in order to rebuild the depleted stocks, not more than 5 000 fin whales should be killed, but that if whaling activities were continued at the 1962/63 rate about 14 000 fin whales would be caught, equivalent, including catches of other whales, to some 8 500 Blue Whale Units (BWU). Members of the Commission were unwilling to make so large a reduction in the quota from that for the 1962/63 season (15 000 BWU), and therefore agreed on a quota of 10 000 BWU for 1963/64. This gave no effective restriction on whaling activities, and the catches were very close to the predicted values (13 870 fin whales, and a total of 8 429 BWU).

Such close agreement between observed and predicted values was partly a matter of luck, that is, certain assumptions made in constructing the model were quite closely fulfilled. In particular the model assumed that some factors influencing the catch, such as the weather and the skill of the gunners were, in the 1963/64 season, close to the average of previous seasons. These assumptions were nearly fulfilled, but a slight difference in weather or in the skill of a few gunners could have increased the difference between observed and predicted catches to perhaps three or four hundred animals. The closeness of the agreement did not prove that the model is correct, or that a slightly different model might not give a rather closer fit, but does prove that the model used can predict within useful limits the results of one pattern of whaling activity. Presumably the model could also predict the results of other patterns of activity, and in particular the result of a severe restriction in catches for a period long enough to allow the stocks to rebuild. Therefore the model serves as a usable basis for managing the whale resources.

As in the whale example, most models include simplifying assumptions about the factors which are not of immediate interest (e.g. weather), usually stated, when stated explicitly, in the form "assuming the conditions are constant." This should not be taken to mean that the validity of the model depends on the constancy of these conditions, and that the model should not be used if conditions vary. Rather it means that for the purposes for which the model has been constructed, the variations caused by these conditions are not of primary interest, and will be ignored.

This manual is mainly concerned with studying the effect of fishing on the stocks and on the catches; it is, therefore, essentially concerned with the long-term effects. Also when predicting the catch from a given pattern of fishing the important question is often not the absolute amount of catch but the catch relative to that which would have been taken with some other pattern of fishing. Many fluctuations and variations are therefore irrelevant to the purposes of this manual. For in-

stance, very often the average catch per trawl haul is taken as a measure of the abundance of the stock; the actual catch taken in one haul will depend on a large number of factors, e.g. the size of the trawler, the skill of the skipper, the precise ground, the season, the weather and the time of day, some of which may have a considerably greater influence on the catch of that particular haul than the overall abundance of the stock. Fish population dynamics is not however concerned with studying or predicting the catch of one haul, but the average catch over a period, say a year. Most of these factors will have average annual values which are effectively constant from year to year, and thus can be ignored; only if these annual values vary, and particularly if they show a trend (e.g. an increase in the average size of trawler) may they have to be studied in detail.

When comparing the catches from two different patterns of fishing, e.g. trawling with large or small meshes in the cod-end, even year-to-year fluctuations can often be ignored. For instance, variations in recruitment may make big differences to the catch in any one year, but will not in general affect the conclusion that say with the present amount of fishing, the use of meshes of 120 mm in the cod-end will give sustained catches 5 percent larger than those taken when meshes of 110 mm are used.

Any model will eventually have to be replaced or modified, possibly merely by adding a little complexity to take into account further factors (e.g. weather conditions in the whale example above) to attain rather greater precision, or perhaps being replaced by a different model. In any case, the process of construction of a model, testing it, and modifying or replacing it is an essential part of the study and eventual understanding of the dynamics of fish populations, or indeed any subject of scientific study. The process of model construction is the complement of the collection of data, and in fact it is only by constructing and using models that it is possible to decide what data should be collected.

The basic model used in nearly the whole of this manual is one in which the stock considered is taken as being self contained, and the various factors causing the stock to change are considered separately. These factors are as follows:

Recruitment (see section 7)

Growth of individuals (see section 3)

Deaths due to fishing; these will be determined by the fishing effort (see sections 4 and 5.3)

Deaths due to other causes (see section 5)

The changes with age in these factors and in the total weight of a year-class are illustrated in Figure 1.1. This shows the growth in weight of the individual; the decrease in the numbers of individuals (the full line shows the decrease in the absence of fishing, the broken line the decrease if fishing occurs after some age, t_c); and the total weight

of the stock. The last has a maximum at some intermediate age, the "critical" age of Ricker.

In the early sections each of these factors are considered separately, and the models are developed to describe each in quantitative terms. In the final sections the factors are combined to provide a quantitative model for the changes in total weight of the stock, and in catch, for various patterns of fishery. The modifications to the model which are necessary to take into account interactions between the various factors, e.g. that increased fishing will reduce the stock and therefore may affect the recruitment, are discussed briefly in section 11.

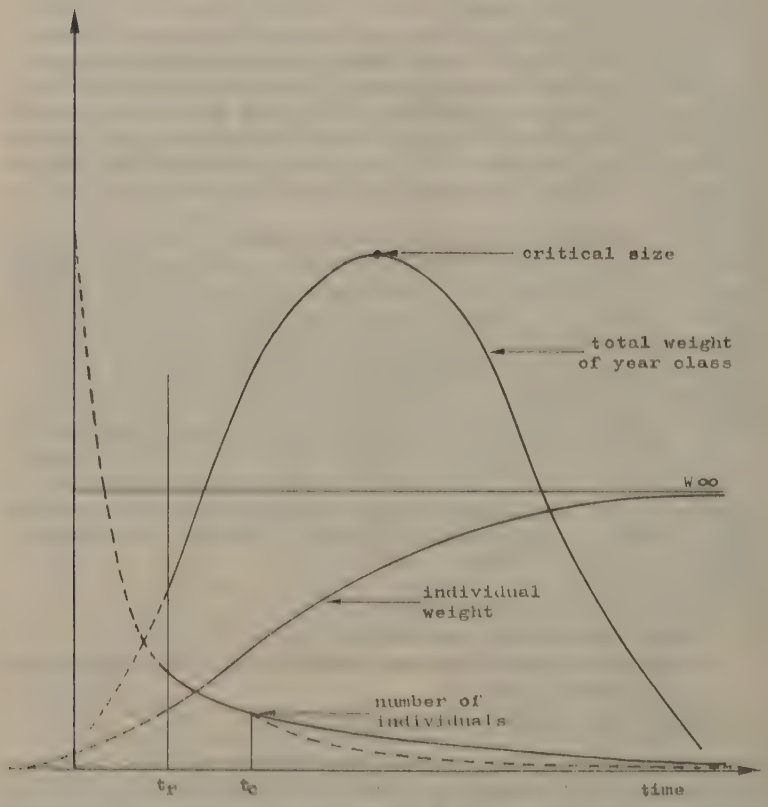

FIGURE 1.1 Changes in numbers and weight of a year-class of fish during its life.

A. ESTIMATION OF PARAMETERS

SECTION 2. MATHEMATICS, STATISTICS AND SAMPLING

2.1 Mathematics

2.1.1 Introduction

In the analysis of a fishery and in stock assessment one is mainly interested in changes. They can be changes in the number of a stock with time, changes in weight of a fish with age, changes in yield with changes in the fishing effort, etc.

Changes with time are measured as rates, i.e. the change in the magnitude of the quantity (weight, etc.) considered divided by the period of time during which it occurred. Even if the time interval is not explicitly specified, unit time (e.g. one year) is usually to be inferred and thus the change is implicitly a rate.

In mathematical terms, if for a period of time Δt, a variable y changes by the amount Δy, then the mean rate of change during this period is $\Delta y/\Delta t$. This rate is an absolute rate. A relative rate can be obtained by dividing the absolute rate by the value of the variable at some point during the period, e.g. at the beginning, when it becomes $\frac{1}{y}\frac{\Delta y}{\Delta t}$. These concepts can be generalized taking t as any variable, not necessarily time.

Theoretical models have the advantage of permitting the analysis of the influence of some factors by studying the mathematical properties of the models. For mathematical simplicity in these models and elsewhere instantaneous rates are often used.

Instantaneous rates can be taken as the limit of the mean rates when the period of time, Δt, tends to zero. Mathematically this is equivalent to the concept of the derivative.

The hypotheses to be made on the relationships between instantaneous rates and the variables can be expressed in the form of differential equations. The differential and integral calculus are important mathematical tools in the analysis of the dynamics of population and other systems. Some of these hypotheses lead to the exponential, logarithmic and power functions.

For the above-mentioned reasons a quick review of powers, exponential and log functions, as well as of differential and integral calculus, is important. Granville, Smith and Longley's *Elements of the differential and integral calculus* deals extensively with such matters.

2.1.2 Functions

Let x and y denote two variables. If to each value of x corresponds a value of y then we can say that y is a function of x or symbolically $y = f(x)$. Graphically, if we plot the values of x on the abscissa (horizontal) axis and the corresponding values of y on the ordinate (vertical) axis, the curve joining the points, $P(x, y)$, with abscissa x and ordinate y, is a graphical representation of the function $y = f(x)$:

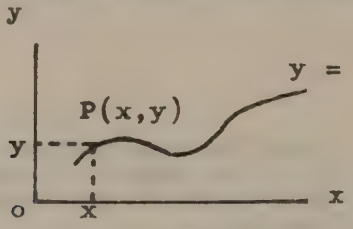

Figure 2.1.

Perhaps the simplest and one of the most used functions is the linear function $y = a + bx$ where a and b are constants. Its graphical representation is a straight line with the intercept on the axis of y equal to a and the slope equal to b :

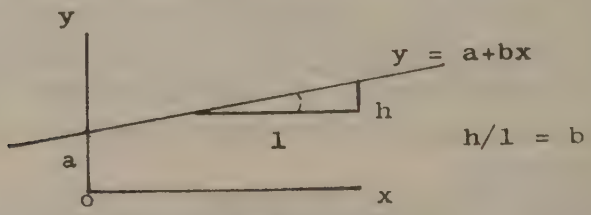

Figure 2.2.

When $a = 0$ then $y = bx$, which represents a straight line passing through the origin. This relationship states that y and x are directly proportional (Figure 2.3.1). For the special case $b = 1$, the equation $y = x$ is the bisector of the positive quadrant (Figure 2.3.2).

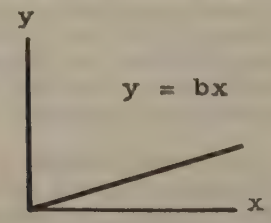

Figure 2.3.1.

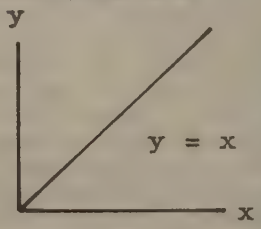

Figure 2.3.2.

The figure below shows the position of the straight line for different values of b

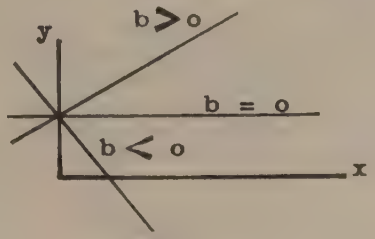

FIGURE 2.4.

Another way of writing the linear function is:

$$y - y_o = b\,(x - x_o) \text{ where } (x_o\,,\, y_o) \text{ is one point of the line.}$$

This form is especially useful when we know two points of the line and we wish to formulate the equation. Thus, if one point is $(x_o\,,\, y_o)$ and the other is $(x_1\,,\, y_1)$ the line will pass through both if b satisfies the equation $y_1 - y_o = b\,(x_1 - x_o)$, that is, $b = (y_1 - y_o)/(x_1 - x_o)$. The equation can then be written immediately.

In a linear function the mean absolute rate of change of y with x is constant and equal to the slope. Thus the instantaneous absolute rate is also constant and its value is the slope b.

For any other function the mean absolute rate between two values x_o and x_1, is the slope of the straight line passing through the points $(x_o\,,\, y_o)$ and $(x_1\,,\, y_1)$

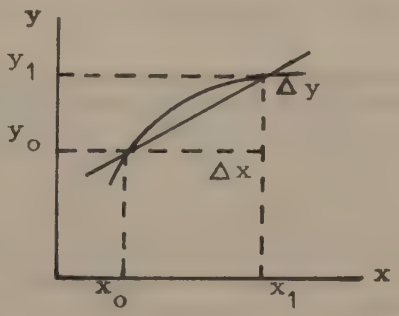

FIGURE 2.5.

$$\frac{(y_1 - y_o)}{(x_1 - x_o)} = \frac{\Delta y}{\Delta x} = \text{slope} = \text{mean absolute rate}$$

Another very useful function is the parabola, also called the second degree polynomial, $y = a + bx + cx^2$

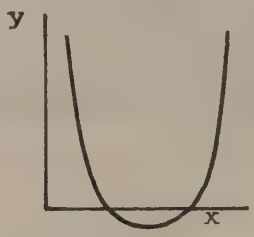

FIGURE 2.6.

The equation can sometimes be written in the form:

$y = A(x - x_o)(x - x_1)$ where x_o and x_1 are the intercepts on the x-axis and the sign of the constant A determines whether it is concave upward or downward.

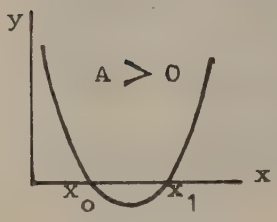

FIGURE 2.7.1.

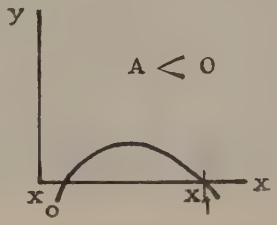

FIGURE 2.7.2.

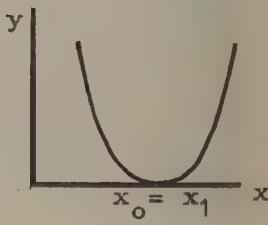

FIGURE 2.7.3.

The exponential function $y = a^x$ where a is a positive constant has the graphical representation shown in Figures 2.8.1 and 2.8.2.

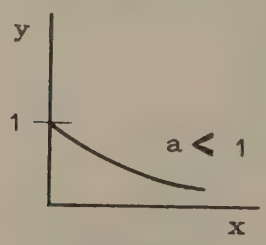

FIGURE 2.8.1.

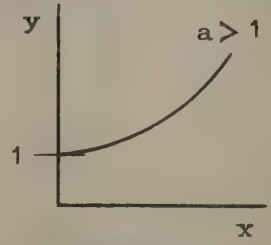

FIGURE 2.8.2.

An exponential function commonly used for its mathematical convenience is the one with a equal to the mathematical constant e (see page 14).

Some curves have an asymptote, i.e. a straight line to which the curve approaches closer and closer as x becomes extremely large (or extremely small); more precisely they are tangents to the curve when $x = \infty$ (or $-\infty$). For example: $y = a^x$ with $a < 1$ (see Figure 2.8.1) has the asymptote $y = 0$; the curves $y = 1 - e^{-x}$ and $y = 1 - e^{-2x}$ both have the asymptote $y = 1$, the second one approaching this asymptote rather more quickly.

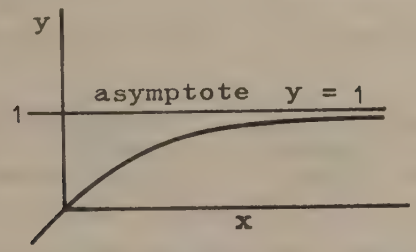

FIGURE 2.9.

The representation of the relationship between two variables may often be simplified by transforming one of the variables, i.e. by using some function of the variable rather than the variable itself. Thus if we are considering the relation: $y = A/x$, this may be transformed into a direct proportional relationship using the variable $w = \frac{1}{x}$, then $y = Aw$.

It is always possible to transform a mathematical function into a straight line relation by a suitable transformation of variables. This is often useful when fitting a theoretical, and possibly complicated curve to observed data; the fitting of a straight line, either graphically by eye, or by regression techniques is relatively simple. Fitting more complex curves, e.g. the exponential, is more difficult, either by eye or by calculation. It should be noted that the least square regression (or other fitted curve) which uses the arithmetic means of the transformed variables will probably not coincide with the arithmetic mean of the original variables, e.g. using the transformation $w = \log x$, the arithmetic mean of the w's is the geometric mean of the x's.

As we will see later (page 58), the curve relating the number of fish of a year-class alive at time t can be expressed as $N_t = N_0 e^{-Zt}$ and can be transformed into the straight line $y = a + bt$, where

$a = \log_e N_o$ and $b = -Z$, using the logarithmic transformation $y = \log_e N$.

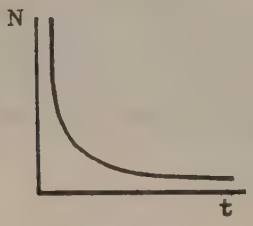

FIGURE 2.10.1.

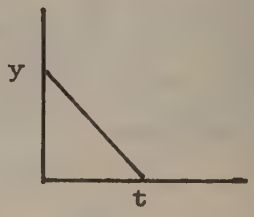

FIGURE 2.10.2.

The functional relationship $y = f(x)$ can also be expressed in the inverse way, that is expressing x as a function of y, $x = g(y)$. For instance, the linear relation $y = a + bx$ can be expressed in the inverse form (also linear) $x = -a/b + \frac{y}{b}$ (provided $b \neq 0$). If the function $f(x)$ is other than a simple linear one, it may happen that more than one value of x will give the same value of y; then the inverse function $x = g(y)$ will not be a simple single valued function. For instance, if $y = x^2$, then the inverse function is $x = \pm\sqrt{y}$. Graphically, the representation of a function and its inverse are identical. Given a graph of $y = f(x)$ this can be used as a graph of $x = g(y)$ by a simple interchange of axes.

2.1.3 POWERS AND LOGARITHMS

A power is represented by two numbers and written symbolically as a^n, where the number a is called the base and n the exponent. When the exponent is a positive integer, a^n is defined as the product of n factors each equal to a; when the exponent is 0, then a^0 is defined as equal to 1; when the exponent is a fraction, let us say $\frac{p}{q}$, then by definition $a^{p/q} = \sqrt[q]{a^p}$; when the exponent is negative, let us say $-m$, then by definition $a^{-m} = \frac{1}{a^m}$.

When the base is positive the power is positive, but when the base is negative the power is positive if the exponent is even and negative if the exponent is odd.

It is useful to consider the value of a power when the exponent n increases without limit.

If the base a is greater than 1 then a^n also increases without limit.

If the base a is equal to 1 then a^n is equal to 1 for all values of n.

If the base a is smaller than 1 (and positive) then a^n tends to 0.

Some useful rules for multiplying or dividing powers are:

— Powers with the same base

$$a^n \times a^m = a^{n+m} \qquad \frac{a^n}{a^m} = a^{n-m}$$

— Powers with the same exponent

$$a^m \times b^m = (ab)^m \qquad \frac{a^m}{b^m} = (a/b)^m$$

To raise a power to an exponent, the base is raised to the product of the exponents:

$$(a^n)^m = a^{nm}$$

The function $y = a^n$ can be considered in two ways depending on whether the base a, or the exponent n is considered as the variable of interest. In the form $y = x^n$ (i.e. the base is the variable) it is called a power function; in the form $y = a^x$ (i.e. the exponent is the variable) it is called an exponential function.

The inverse function of a power is a root and the inverse function of an exponential is a logarithmic function. Thus if $y = a^x$ then $x = \log_a y$, or x is the logarithm of y to the base a.

When the base is the constant e, the logarithms are called natural or Napierian (or hyperbolic).

From the definition above one can see that the properties of the powers will imply corresponding properties of the logarithms, e.g.

$\log_a (A.B) = \log_a A + \log_a B$ corresponds to the property $a^x \cdot a^y = a^{x+y}$

$\log_a (A/B) = \log_a A - \log_a B$ corresponds to the property $\frac{a^x}{a^y} = a^{x-y}$

$\log_a (A^m) = m \log_a A$ corresponds to the property $(a^x)^y = a^{xy}$

Special relations can also be obtained, such as $\log_a 1 = 0$ and $\log_a a = 1$. The relation between the logs of a number on two different bases, a and b, is:

$$\log_a N = \log_b N \cdot \log_a b$$

The bases most used for logs are the base 10 and the base e ($e \approx 2.72$), the former because 10 is the basis of the numerical system currently used and the latter because this results in the most simple form of several mathematical relationships. From the above relation the logarithm of a number to the base e can be obtained from the logarithm of the number on base 10 multiplied by $\log_e 10 \sim 2.303$. This is a useful expression if a table of natural logs is not available. One of the advantages of using the base 10 is that any number can be expressed as the product of a power of 10 and a number between 1 and 10, e.g. $283.5 = 10^2 \times 2.835$; $0.0053 = 10^{-3} \times 5.3$. In this way the decimal log of any number will be the sum of the decimal log of a number between 1 and 10 (mantissa) plus the decimal log of a power of 10, that is, its exponent (characteristic).

From the above examples this would give $\log_{10} 283.5 = 2 + \log_{10} 2.835$ and $\log_{10} 0.0053 = -3 + \log_{10} 5.3$. The logarithms to base 10 of the numbers between 1 and 10 are given by tables.

Tables of natural logarithms are usually available over a wider range (perhaps from 0.1 to 100) but natural logarithms can be obtained by a similar method for any range from tables of the natural logarithms from 1 to 10. For instance,

$$\log_e 283.5 = 2 \log_e 10 + \log_e 2.835 = 2 \times 2.303 + 1.042 = 5.648 \text{ and}$$

$$\log_e 0.0053 = -3 \log_e 10 + \log_e 5.3 = -3 \times 2.303 + 1.667 = -5.242$$

2.1.4 Derivatives

As already stated, the concept of derivative is equivalent to the absolute instantaneous rate and this is the limit of the absolute mean rate during an interval when the length of the interval tends to zero.

Let us consider a function $y = f(x)$. If x is given an increment Δx, y will have an increment Δy. The limit of the quotient of the increments, $\frac{\Delta y}{\Delta x}$, when Δx tends to zero will be the derivative of y with respect to x at the point (x, y). This can be represented by the symbols $\frac{dy}{dx}$ or y' or $f'(x)$.

Graphically, the incremental ratio $\frac{\Delta y}{\Delta x}$ is the slope of the secant to the curve passing through the points (x, y) and $(x + \Delta x, y + \Delta y)$ and the derivative $\frac{dy}{dx}$ is the slope of the tangent to the curve at the point (x, y) (the tangent is the limit of the secant when Δx tends to zero and $x + \Delta x$ tends to x).

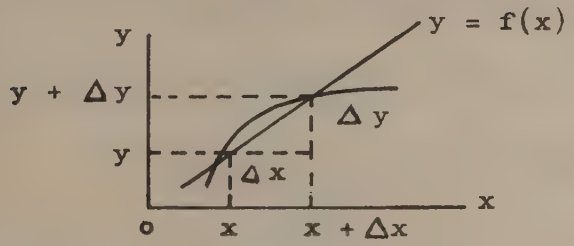

FIGURE 2.11.1.

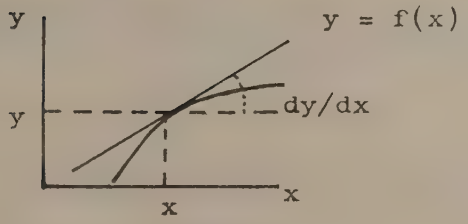

FIGURE 2.11.2.

Thus derivative, absolute instantaneous rate and slope of the tangent are equivalent concepts expressed from different viewpoints. Using this definition, we can calculate the derivative of a function. For instance, to determine the derivative of $y = 3x^2$ we can start by calculating the increment of y for a given increment of x. We obtain the value of the function at the point $x + \Delta x$ and subtract from the value of the function at the point x:

at x $\qquad y = 3x^2$

at $x + \Delta x$ $\qquad y + \Delta y = 3(x + \Delta x)^2 = 3x^2 + 6x\Delta x + 3\Delta x^2$

then $\Delta y = 6x\Delta x + 3\Delta x^2$

The incremental ratio will be $\frac{\Delta y}{\Delta x} = 6x + 3\Delta x$. As Δx becomes very small, the second term on the right will also become small and in the limit as $\Delta x \longrightarrow 0$ this second term also tends to zero, so that $\frac{dy}{dx}$ will be equal to $6x$.

Derivatives can be arrived at easily if we obtain, in that way, some rules, e.g.

Derivative of a constant, c, is zero:

$$\frac{dc}{dx} = c' = 0 \text{ (note that differentiation is often denoted by a dash')}$$

Derivative of a variable x with respect to itself is:

$$\frac{dx}{dx} = x' = 1$$

Derivative of the product of a constant c and a function $u(x)$ is the product of the constant and the derivative of the function:

$$(cu)' = cu' \quad \text{e.g.} \quad \frac{d(3x)}{dx} = 3$$

Derivative of a sum of two functions, $u(x)$ and $v(x)$, is the sum of their derivatives:

$$(u + v)' = u' + v' \quad \text{e.g.} \quad \frac{d(3x + 2)}{dx} = 3 + 0 = 3$$

Derivative of a product of two functions, $u(x)$ and $v(x)$, is given by

$$(u.v)' = u'v + u.v' \quad \text{e.g.} \quad \frac{d(3x^2)}{dx} = \frac{d(3x.x)}{dx} = 3.x + 3x.1 = 6x$$

Derivative of a power of a function $u(x)$ is given by

$$(u^n)' = nu^{n-1}u' \quad \text{e.g.} \quad \frac{d(3x + 1)^2}{dx} = 2(3x + 1)\cdot 3 = 6(3x + 1)$$

Derivative of the quotient of two functions, $u(x)$ and $v(x)$, is given by

$$\left(\frac{u}{v}\right)' = \frac{u'v - uv'}{v^2} \quad \text{e.g.} \quad \frac{d\left(\frac{x}{2x+1}\right)}{dx} = \frac{1.(2x+1) - x.2}{(2x+1)^2} = \frac{1}{(2x+1)^2}$$

We can also obtain from further analysis the derivative of special functions often used in fisheries studies, such as

$$(e^x)' = e^x$$

$$(e^u)' = e^u u'$$

$$(\log_e u)' = \frac{u'}{u}$$

It is interesting to note that the derivative of the function e^x is e^x itself; it is this property of the exponential of base e which makes it so important on theoretical grounds.

The derivative of the function $y = e^{ax}$ is $y' = e^{ax}a = ay$; this means that the derivative, or the instantaneous rate, of y is proportional to y, a property very useful in many situations (e.g. studies of growth, mortality, etc.).

As an example of how we could apply these rules let us calculate the derivative of $y = (3 + e^{2x})(1 - x^2)$.

Applying the rule for a product we can write

$$\frac{dy}{dx} = (3 + e^{2x})'(1 - x^2) + (1 - x^2)'(3 + e^{2x})$$

To calculate the derivative of the first factor we can apply the rule concerning the sum of two functions, then $(3 + e^{2x})' = (3)' + (e^{2x})'$. We thus see that $(3)' = 0$ and $(e^{2x})' = e^{2x}(2x)' = e^{2x}.2$ and thus $(3 + e^{2x})' = 2e^{2x}$. Calculating the derivative of the other factor: $(1 - x^2)' = (1)' - (x^2)' = 0 - 2x = -2x$. Finally $y' = 2e^{2x}(1 - x^2) - 2x(3 + e^{2x})$.

The derivative of a function of x is, in general, another function of x. This function may also be differentiated to give another function of x. This last is called the second derivative of the original function. It is usually represented by the symbols y'' or d^2y/dx^2 and could be interpreted as the absolute rate of the absolute rate, which in physics is called acceleration. Third, fourth, etc. derivatives can also be defined.

An application of the first derivative is the analysis of the change of a function and of the second derivative the analysis of the rate at

which this change is itself changing. For the points where y' is positive, y is increasing, and where y' is negative, y is decreasing. If $y' = 0$, y is a stationary point. When y'' is positive the slope of the curve is increasing and the graph of y is concave upward; when y'' is negative the slope of the curve is decreasing and the curve is concave downward. If $y'' = 0$, y is an inflection point (unless y' was also 0). From the sign of y'' we can decide if the stationary points are maxima or minima.

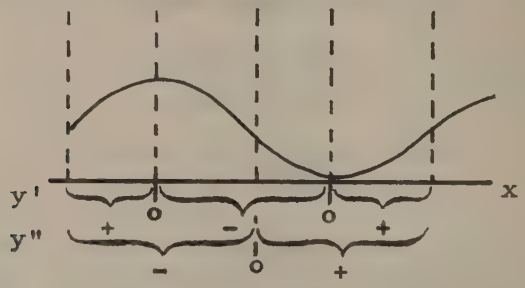

FIGURE 2.12.

2.1.5 INTEGRALS

In the last section we saw how, given a function, we could obtain its derivative. The reverse problem would be to obtain the function knowing its derivative. This operation is called integration and the function so obtained is called the integral. For instance, what is the integral of $3x^2$? We have seen that the derivative of x^3 is $3x^2$, thus an integral of $3x^2$ could be x^3. But so also is $x^3 + 4$ or generally $x^3 + C$ where C is any constant, since the derivative of a constant is zero. This means that the integration of a function does not produce a simple function but a family of functions defined by the additive, arbitrary constant C.

The integral of $f(x)$ is represented by $\int f(x)\,dx$ or $F(x) + C$ and is called the indefinite integral. It is indefinite because of the arbitrary constant C.

The rules of integration can easily be obtained from the rules of differentiation, as they are inverse operations. Thus

$$\int a dx = ax + C$$

$$\int dx = x + C$$

$$\int audx = a \int udx$$

$$\int x^n dx = \frac{x^{n+1}}{n+1} + C \text{ (for } n \neq -1)$$

$$\int \frac{1}{x} dx = \log_e x + C$$

$$\int e^x dx = e^x + C$$

Useful expressions are

$$\int f'(x)\, dx = f(x) + C$$

$$\int (u + v)\, dx = \int udx + \int vdx$$

$$\int (u'v)\, dx = u.v - \int uv'dx$$

A technique very useful for integration is the change of variable. For instance to integrate e^{4x-3} we can put $v = 4x - 3$ and $dv = (4x - 3)'\, dx$ or $dv = 4\, dx$. Then

$$\int e^{4x-3}\, dx = \int e^v \frac{dv}{4} = \frac{1}{4} \int e^v\, dv = \frac{1}{4} e^v + C \quad \text{or} \quad \frac{1}{4} \cdot e^{4x-3} + C.$$

If one knows a value of the integrated function it is possible to determine the corresponding value for the constant C. In general terms we can say that if $y = F(x) + C$ is the integral of a function, and knowing that (x_o, y_o) is a point of the integral curve then $y_o = F(x_o) + C$ and $C = y_o - F(x_o)$; thus $y - y_o = F(x) - F(x_o)$ gives the curve which satisfies the conditions of the problem.

We have seen the integration as the inverse operation of differentiation. There is however another concept of integral. This concept can be easily understood through the calculus of areas, which is one of the most important applications of integrals. Let us, for instance, cal-

culate the area under the curve $y = f(x)$, the axis of abscisses and the ordinates at $x = a$ and $x = b$.

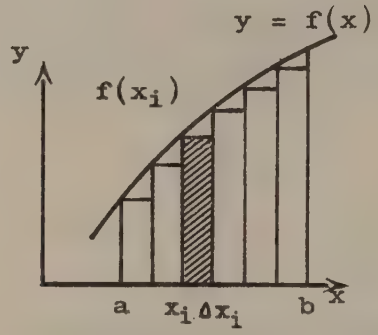

FIGURE 2.13.

This area can be approached by the sum of the areas of the rectangles of base Δx_i and height $f(x_i)$, this is $\Sigma f(x_i)\,\Delta x_i$, where the interval from a to b was subdivided in n small intervals Δx_i. The limit of this sum when the number of subdivisions increases indefinitely and each interval decreases to zero can give the area required. This limit is then the definite integral. This definite integral, $g(x)$ is one possible value of the indefinite integral, since the rate at which the area under curve increases as x increases is equal to the height of the curve, so that $\frac{dg(x)}{dx} = f(x)$. The area under the curve between $x = a$ and $x = b$ is written $\int_a^b f(x)\,dx$.

To calculate the definite integral we calculate as before the indefinite integral and subtract its value for $x = b$ and for $x = a$, this is:

$$\int_a^b f(x)\,dx = [F(x)]_a^b = F(b) - F(a)$$

As an example let us calculate the area under the function $y = 3x^2 + 5$ between $x = 2$ and $x = X$.

$$\int_2^X (3x^2 + 5)\,dx = [x^3 + 5x]_2^X = (X^3 + 5X) - (2^3 + 5 \times 2) = X^3 + 5X - 18$$

(Note that when calculating geometrical areas the values of the function and of its integral must be taken as positive.)

Another very important application of integrals is in solving differential equations. A differential equation is an equation with derivatives or differentials, for instance, $y' = 4x - 2$ or $dy = (5 + 2x)\,dx$.

Differential equations can be very difficult to solve, but some elementary processes are applicable to easy equations. One of these processes is called the separation of variables. For instance, let us integrate the equation $dy = xydx$. By a simple operation we can obtain (separate) all the expressions with the variable y in a member of the equation and the expressions with the variable x in the other: $\frac{dy}{y} = xdx$. Now each member can be integrated separately:

$$\int \frac{dy}{y} = \int xdx$$

or $\log_e y + C = \frac{x^2}{2} + C$ or, joining the arbitrary constants, $\log_e y = \frac{x^2}{2} + C$

The same result could be presented in a slightly different way by, instead of the constant C, using arbitrary point (x_o, y_o), thus

$$\int_{y_o}^{y} \frac{dy}{y} = \int_{x_o}^{x} xdx \quad \text{or} \quad \left[\log_e y\right]_{y_o}^{y} = \left[\frac{x^2}{2}\right]_{x_o}^{x}$$

and

$$\log_e y - \log_e y_o = \frac{x^2}{2} - \frac{x_o^2}{2} \quad \text{or, alternatively,} \quad y = y_o\, e^{\frac{1}{2}(x^2 - x_o^2)}$$

This last expression can be very useful when one is interested in pointing out some special point of the function.

2.2 Statistics

Fish population studies involve the measurement and analysis of many quantities — e.g. age compositions, and growth rates — few of which can be measured exactly, either because of their inherent variability or the difficulty of measurement. Statistics must therefore be used to

some extent, if only in such a simple form as taking the mean of a set of values. Basic statistical methods are the same whatever the subject in which they are being applied, and are described in many textbooks. These notes will therefore only deal very briefly with the basic methods. Some applications, e.g. correlation and regression analysis will be dealt with later as they occur. In this section most attention will be paid to the problem of sampling fish populations. (Statistics is dealt with in more detail in another manual in this series, in which both the basic methods and special applications to fisheries are described.)

In statistics we are concerned not so much with any individual value, e.g. the size of any one particular fish on the fish market, but with the frequency with which the various values (e.g. size of fish) occur. Such frequency distributions may be represented graphically, either as histograms or frequency polygons. Much of the frequency distributions can be described by two quantities; the average value (or the position of the curve) and the spread. The most common measures for the average are the arithmetic mean (or simply mean), the median (or half way value) and the mode (or most frequent). Of these the mean has most advantages. The common measure of dispersion is the variance, which is the average of the square of the deviation from the mean; the square root of the variance is the standard deviation. Further discussions of these measures, together with methods of calculation etc. may be found in most textbooks, e.g. Yule and Kendall (1950), chapters 4, 5 and 6.

Tests of significance are another group of statistical tools of great use in fishery research, as in most other fields. While the explanation of the arithmetical steps involved in any particular test will be left to the appropriate section of the textbooks, e.g. Yule and Kendall (1950), chapter 21, it is worth emphasizing here the underlying basis of tests of significance. That is, we assume some null hypothesis, and on this basis calculate the probability of the observed values occurring. If this probability is sufficiently small (usually one in twenty, or one in a hundred) we reject the null hypothesis. For instance, using the *t*-test for the difference in the means of two samples, the null hypothesis is that the two samples come from the same population. If the probability of a value of t equal to or greater than that observed occurring is say 0.01, this means that if the two samples had come from the same population, an unlikely event (a one in a hundred chance) has taken place and we therefore believe that the two samples did not come from the same population, i.e. they are statistically different. Such a test does not give any information on the probability of the two samples coming from different populations, or on the practical significance of the difference. For instance, two small and variable samples may differ by an amount which is not statistically significant, but which if real would be most important. Conversely, for two large and homogeneous samples a difference may be large enough to be statistically significant, but yet so small as to be negligible in practice.

2.3 Sampling

(For further details see FAO. *Manual of sampling and statistical methods for fisheries biology*, by J.A. Gulland. Part 1. *Sampling methods.* Rome, 1966.)

2.3.1 General

Most of the quantities involved in fish population work cannot be obtained or measured throughout the whole population; e.g. it is virtually impossible to measure all fish caught, even less all the fish in the sea. A section, or sample, of the whole population is therefore examined for the attributes concerned, e.g. percentage of mature fish, or average size. On the assumption that this sample is representative of the whole population, an estimate may be made of the true value in the population. If the sampling system used is a good one, then the estimate obtained will differ little from the true value. The merits or otherwise of a sampling system can therefore be measured by two quantities relating to the estimates obtained (those measures refer not to any individual estimate, but to the set of estimates which might be obtained by repeated samples); firstly, the variance, which as defined above for any statistical distribution, is the measure of the scatter of the estimates about their mean value; secondly, the bias, which is the extent to which the mean value of the set of possible estimates differs from the true value. (The term bias is also used for the processes leading to this difference.)

Because when a bias exists, it exists in all samples, tending to make the estimates constantly greater (or less) than the true value, it cannot be detected as a difference between repeated samples; thus in general bias is very difficult to detect, and hence eliminate, in subsequent analysis. A large variance, in contrast, appears at once in the differences between samples. Large bias is therefore even less desirable than large variance, in that it may cause what appear to be reliable and consistent data to give results that are consistent only in the extent to which they are wrong.

The basic feature of any good sampling system is a "random" sample. The aim of a random sample should be to ensure that all members of the collection of objects being sampled have the same chance of occurring in the sample. In practice this condition may be relaxed and the sampling be nonrandom so long as there is no relation between the chance of occurring in the sample, and the value of the attribute being measured. For instance, the first fish unloaded from a trawler onto the fish market is usually one of the last caught and will be placed near the edge of the array of fish and therefore have a better chance of appearing in the sample. If we are only concerned with sampling for the size of fish, this may not matter as there is little relation be-

tween size of fish and time of capture, but the sample would be a very bad one if we were concerned with the condition or freshness of the fish. The main damage done by nonrandom sampling is this introduction of bias (e.g. that the sample taken above will be biased toward having too many fresh fish) though nonrandom sampling has other disadvantages, e.g. that many of the calculations used for estimating variance etc. are only valid for random samples. The first concern in taking a sample is therefore to ensure that no form of selection can occur that might cause a bias. Such selection may be very obvious and direct, e.g. the tendency to take the bigger fish from a pile, leaving the smaller until last, but may be much less obvious; e.g. in the East Anglian herring season it would seem convenient to take samples of herring from the first drifters arriving each morning. These tend to be from the nearer grounds, which in turn tend to have slightly different size and age of fish. Thus a nonrandomness in time of sampling may cause a bias in the estimate of average size or age of fish landed.

The practical difficulties in taking a truly random sample from a large and heterogeneous collection of objects are considerable. These difficulties may be overcome by dividing up the whole collection into smaller and more compact sections, within which a random sample may be taken fairly readily. Two such methods of sampling are stratified and two-stage sampling. In stratified sampling the whole collection of objects is divided into several sections, or strata, each of which is then sampled and analysed separately, e.g. landings at different ports may be taken as strata. This method is particularly useful in reducing bias and variance when there is a marked difference between strata.

2.3.2 Sampling the landings

The chief sampling problem in fish population studies occurs when estimating indices of abundance of the different ages and sizes of fish, and particularly in sampling the commercial catches for size and age composition. Before starting to consider the sampling procedure, the objective of the sampling must be defined, both in extent and the attribute being examined, e.g. length of plaice landed by United Kingdom trawlers from the North sea. Following a stratified sampling scheme the complete population, which will be rather heterogeneous, may then be divided into fairly uniform strata. For United Kingdom demersal landings it was found suitable to treat landings at each port and in each month separately, but for the more variable herring landings, landings in three-day periods were chosen. The first step in the actual sampling procedure is to ensure that the sample taken is not biased. Once the catch of a vessel is sold it may be divided among a number of merchants each of whom is almost certain to prefer a certain size or quality of fish; therefore any sample from the purchases of one merchant

is almost certain to be biased. Sampling of commercial catches must therefore be taken before the catch is divided; in the United Kingdom this means sampling in the early morning while the catch is laid out on the fish market before being auctioned.

The choice of fish to measure is conveniently done in two stages; first a sample of one or more ships from the whole fleet landing during the period, and then measuring a sample of fish from the chosen ship or ships. The choice of ships to sample is usually straightforward and minor departures from nonrandom samples are not very likely to be harmful, but may introduce bias when time of landing or position on the market (which are likely to influence their chance of being sampled) are themselves influenced by the fishing ground, and hence related to the composition of the catch. This difficulty may be overcome by further stratification, sampling and analysing the catches from each area separately.

When taking a sample of fish from a ship's catch an important source of bias is the tendency of most people to take first the largest fish from a pile and to leave the smallest to last. This is especially noticeable when sampling fish on deck, e.g. a haul of a research vessel. At sea this bias can only be overcome by handling all the catch, or at least a predetermined part (e.g. one corner), clearing all the fish right down to deck level. On the market most fish are laid out in boxes (often with the larger fish of the box on top), and bias will be avoided by sampling one or more complete boxes. If there is no definite sorting into two or more categories, systematic differences between boxes are unlikely and a convenient but nonrandom method of sampling, e.g. taking boxes from one edge of the landing, is justifiable. Important in working up the results of such a sampling system are the raising factors, i.e. ratios of weight sampled to total weight landed, both over the whole landings and within a sampled ship. The procedure is as follows; supposing we are interested in the total number landed of a certain size (or age, maturity, etc.) of fish

Let m = number of ships from which samples were taken and for any particular one of these, say the ith,

W_i = weight landed

w_i = weight sampled

n_i = number of fish of required size in sample

then $\frac{W_i}{w_i} = r_i$ = raising factor for ith ship

and hence $n_i r_i = n_i \frac{W_i}{w_i}$ = number of fish of required size in sampled ship.

Adding up for all sampled ships gives the number of fish of required size for all sampled ships, as $n = \sum_{1}^{m} n_i r_i$

Also if W = total weight landed

and w = weight landed by sampled ships

then R = raising factor $= \frac{W}{w}$

and $Rn = n\frac{W}{w}$ = total number of fish of required size landed

$= N$ say.

That is $N = \frac{W}{w} \Sigma \frac{n_i W_i}{w_i}$

Frequently fish are sorted into several size categories which may or may not be the same from one ship to the next; then obviously a sample must be taken from each category of the ship examined. The figure for the ship as a whole is then given by raising each category individually by the appropriate raising factor. Thus, supposing there are two categories, using the notation above, and using one or two dashes to distinguish the different categories, we have

$$r'_i = \frac{W'_i}{w'_i} \; ; \quad r''_i = \frac{W''_i}{w''_i}$$

and number of fish of given size on the ith sampled ship is

$$n'_i r'_i + n''_i r''_i = n'_i \frac{W'_i}{w'_i} + n''_i \frac{W''_i}{w''_i}$$

Then the total number landed may be estimated directly as

$$N = R \Sigma \left\{ n'_i r'_i + n''_i r''_i \right\}$$

Alternatively, and rather better, the sorting by categories can be used as stratification through all landings, and raising factors for each category calculated and applied. Then the estimate of the numbers landed is

$$N = R' \Sigma n'_i r'_i + R'' \Sigma n''_i r''_i$$

Where

$$R' = \frac{W'}{w'} \; ; \quad R'' = \frac{W''}{w''}$$

This second estimate will be more precise (have less variance), as it utilizes the information on the division of all landings between the categories. It can be applied so long as the sorting is constant even if not very accurate, i.e. the number and definition of the categories is constant, even if the dividing line between them is variable.

In population studies we are interested in several characteristics of the fish, e.g. length, weight, age, maturity, most of which are closely related. Some, e.g. lengths, are very easy to determine both quickly and accurately even under the somewhat adverse conditions at sea or on the fish market. Other characteristics, e.g. age, which are considerably more tedious to determine are then most easily determined by sampling directly for length only, and using relatively small age samples to establish an age-length key for converting length composition to age composition. That is, the length sampling gives the number of fish in each length group, and the age samples give the proportion of each age within each length group. The number at each age is then readily given; algebraically if

N_i = number of fish in ith length group

P_{ij} = proportion of fish of age j in ith length group

where

$$P_{ij} = \frac{n_{ij}}{n_i}$$

n_i = number of length i examined for age

n_{ij} = number of length i examined which were age j

then

$N_i P_{ij}$ = total number of fish of length i and age j

and

$\Sigma N_i P_{ij}$ = total number of fish of age j.

It should be noted that these calculations involve no assumptions concerning the pattern of growth, though the advantages of the method in form of increased accuracy (decreased variance and risk of bias) are greatest when the growth is fast and uniform.

2.3.3 Sampling the population

Data on the composition of the catch are important in themselves, particularly when comparing and combining the effects of two dissimilar fisheries exploiting the same stock; or in making assessments of the immediate effects of, say, a mesh change. In addition, the catch, whether of the commercial fleet or of a research vessel, may also be considered as a sample of the stock. The usual sampling methods are directly applicable, e.g. stratified sampling by dividing the region into fairly uniform subareas, but special problems arise in obtaining unbiased estimates of the abundance and the composition of the stock. The first is a matter of relating stock density to catch per unit effort, and the second of selection in the widest sense, i.e. including any factor making one size (or condition) of fish more likely than another to be caught and retained by the gear, with mesh selection included as a special case. These latter problems will be discussed more fully in the appropriate later sections.

2.4 Exercises

2.4.1 Mathematics

1. Values of x and the corresponding values of y are given in the table:

x	1	2	3	4	5
y	10	25	32	38	41

   Draw a curve passing through these points. Determine the absolute mean rate of the change of y during the interval $x = 1.5$ $x = 3.5$. Which is the relative mean rate in the same interval? Give the approximate value for the instantaneous absolute rate at $x = 1.5$.

2. Calculate the equation of the straight line passing through the points $A\,(2\,,-5)$ and $B\,(-1\,,3)$. Calculate the intercepts with the co-ordinate axis. Write an equation for a parallel to this straight line.

3. Draw a straight line with negative slope.

4. Calculate the straight line with intercepts -2 with x axis and 3 with y axis. Which value of y corresponds to $x = 6$? To which value of x does $y = 3$ correspond?

5. Calculate, without tables:

$$10^3 \quad 10^{-1} \quad 4^0 \quad 8^{\frac{2}{3}} \quad 25^{-\frac{1}{2}}$$

6. Calculate:

(*a*) $\log_{10} 42.5$ $\log_{10} 0.018$ $\log_{10} 0.263$

(*b*) $\log_e 0.50$ $\log_e 2.52$ $\log_e 17.10$

7. Determine x in:

$$0.70 = e^{-x} \qquad 2.4 = 10^x \qquad 10^4 = e^x$$

8. Transform (using natural logarithms):

$$y = 2x \,.\, e^{4+x} \qquad \text{and} \qquad N = Re^{-Z(t-t_c)}$$

9. Calculate N given:

$$\log_e N - \log_e N_a = -Z(t-t_a)$$

10. Calculate the product:

$$\log_{10} e \times \log_e 10$$

11. Apply logarithm to the following expressions:

$$w = q \,.\, l^3$$

$$x = (A + B) \,.\, C^4$$

$$L_\infty - l_t = L_\infty \,.\, e^{-k(t-t_0)}$$

12. Calculate the value of $\left(1 + \frac{1}{n}\right)^n$ for $n = 1\,;2\,;5\,;10;100$ and $1\,000$. Verify that the results approach the value of $e \simeq 2.718$ as n increases.

13. Calculate $\frac{dy}{dx}$ for the following functions:

(*a*) $y = 3$ (*b*) $y = 4 - 6x$ (*c*) $y = x^{\frac{1}{2}}$ (*d*) $y = \frac{3 + 2x}{5 - x}$

(*e*) $y = (1 + 4x)^3$ (*f*) $y = 4v^2$ with $v = 5x^2 - 2x$

(*g*) $y = e^x$ (*h*) $y = e^{-4x}$ (*i*) $y = \log_e(5 + x)$ (*j*) $y = (1 + e^{2x})(1 - e^{-2x})$

14. Calculate the second derivative of:

$$y = 4x^3 - 5x \qquad y = e^{4x} \qquad y = \log_e (x + 2)$$

15. Given the function $y = 2x\,(3 - x)$ calculate the first and second derivative and determine the point where the instantaneous rate is zero; the intervals where y is increasing and where it is decreasing; the concavity of the function. Draw the function.

16. Using the first and second derivative find possible points of maxima, minima, and of inflection, intervals where the functions are increasing and decreasing, and concavities for the following functions:

$$y = (x - 1)^2 \quad y = \frac{3x}{x + 1} \qquad y = a\,(1 - e^{-bx})^3 \qquad a > o \text{ and } b > o$$

17. Which is the relationship between the absolute instantaneous rate of $\log_e y$ and the relative instantaneous rate of y, y being a function of x.

18. Calculate the instantaneous relative rate of increase of N with respect to t in:

$$N = N_o \cdot e^{-Z(t - t_o)}$$

19. Calculate the instantaneous absolute rate of increase of l with respect to t in:

$$l = L_\infty\,[1 - e^{-k(t - t_o)}]$$

and express it in terms of l.

20. Calculate the instantaneous relative rate of increase of l with respect to t in:

$$\log_e l = \log_e L_\infty \cdot [1 - e^{-k(t - t_0)}]$$

and express it in terms of the variable l.

21. Integrate the following expressions:

$$\frac{1}{x} \qquad 4x \qquad 7 \qquad e^x \qquad 4 - 2x \qquad (x - 1)(2 - 3x)$$

22. Calculate:

$$\int_1^2 x^3\,dx \qquad \int_0^x e^x\,dx \qquad \int_2^x (3+2x)ds \qquad \int_1^x e^{-3x}dx \qquad \int_0^x e^{4-3x}dx$$

$$\int_{-\frac{3}{2}}^{-\frac{1}{2}} (3+2x)^5 dx \qquad \int_1^x \frac{dx}{x} \qquad \int_{\frac{1}{3}}^x \frac{dx}{2-3x}$$

23. Solve the following differential equations:

$dy = 3x\,dx$ with the condition $y = 2$ for $x = 1$

$\frac{dy}{dx} = 4y$ with the condition $y = y_o$ for $x = x_o$

$\frac{dy}{4+2y} = -3dx$ with the condition $y = y_o$ for $x = x_o$

$\frac{dN}{dt} = -ZN$ with the condition $N = R$ for $t = t_c$

$\frac{dl}{dt} = E - kl$ with the condition $l = o$ for $t = t_o$

24. Calculate the area limited by the curve $y = 5x(4-x)$ and the x axis between $x = 1$ and $x = 3$.

25. Let $y = f(x)$ be a function such as the relative instantaneous rate is constant and equal to $-a$. If (x_o, y_o) is a point of the function, obtain the expression of the function.

2.4.2 Statistics and sampling

1. Given the two length-frequency distributions

Length (cm)	10	11	12	13	14	15	16	17	18	19	20
Frequency	1	3	8	16	18	17	12	6	2	1	0

and

Length (cm)	10	11	12	13	14	15	16	17	18	19	20	21	22
Frequency	0	0	4	12	14	10	9	8	4	3	1	1	0

determine the following:

(*a*) Mean

(*b*) Mode

(*c*) Median

(*d*) Variance

(*e*) Standard deviation

(*f*) Standard error of each mean.

Using these results, determine whether the difference between the means exceeds twice (the 5 percent level) or three times (the 1 percent level) its standard deviation. (Note that the mode is most readily determined graphically; the others by calculation.)

2. Repeat exercise 1 for the two distributions:

(*a*) 15, 17, 20, 23, 24, 27, 29, 31, 33, 35, 36, 36, 38, 40, 42, 42, 46, 49, 52, 53, 54, 58, 60, 65, 71.

(*b*) 19, 26, 23, 29, 30, 32, 34, 37, 38, 40, 42, 42, 44, 45, 46, 48, 51, 54, 56, 59, 60, 65, 68, 75.

3. One ten-stone box (63 kilogrammes) of each, of large, medium and small hake were sampled on each of two trawlers. The number recorded, in each 10-cm group, and the weights landed were

Length group		40–	50–	60–	70–	80–	90–	100–	Total	Weight landed
										Boxes
Ship A	large					7	7		14	2
	medium			8	15	3			26	10
	small	2	32	19	1				54	14
Ship B	large					5	4	3	12	23
	medium			4	17	6	1		28	53
	small	1	13	27	4				45	40

The numbers of boxes landed by all ships were large 350, medium 720, small 1 056. Calculate the number and size distribution of the hake landed by the sampled ships, and the total by all ships.

4. The estimated number of male plaice landed in 1955 at Lowestoft in each 5-cm group were:

25–29	30–34	35–39	40–44	45–49
3 991 984	4 155 009	1 232 174	274 972	15 346

The number of male fish whose otoliths were taken, and their estimated ages, were:

Length \ Age	3	4	5	6	7	8	9	10	11 +	Total
25–29	33	82	30	13	8	1				167
30–34	8	48	53	24	34	12	5	1	1	186
35–39	1	14	26	33	42	19	11	10	6	162
40–44		1	8	2	12	5	5	—	3	36
45–49						1	4	—	4	9

Estimate the total number of six-year-old fish landed.

5. Discuss sampling problems and methods as they occur in fisheries with which you are familiar.

SECTION 3. GROWTH

3.1 Growth by length and weight

For population analysis it is desirable to express the growth of fish in a mathematical expression. The basic requirement is an expression which will give the size (in terms of length or weight) at any given age which agrees with the observed data of size at age, and which is in a mathematical form which can be incorporated reasonably easily in expressions for yield. Strictly, most population analysis is concerned more directly with growth rate, i.e. increase in weight or length per unit time, rather than with the size at various ages, because many problems in fishery assessment are essentially a matter of comparing weight gained by growth against that lost by natural mortality. Sometimes, for instance when considering the effect of an increase in size of first capture, it is particularly important to know the rate of growth over a comparatively short part of the total life span — that is, to know how long it will take a fish to grow from the original size of first capture to the new. There are therefore good reasons for preferring, other things being equal, a method of fitting equations to growth rate data, rather than simply size at age.

Other desirable features of a growth equation are that the computational work involved in fitting it to observed data should be small, that the number of constants used should be few, that as far as possible these constants should have some biological meaning, and that if extrapolated to ages beyond those used in fitting the equation, the equation should not lead to unreasonable results.

There exists a considerable and growing literature on growth equations, which covers a wide range of possible equations, none of which seems to be entirely satisfactory in all situations. In fact it is most unlikely that a simple formula would always be able to describe the growth of even a single fish through most of its life, in which there could be greatly different conditions of food supply, reproductive strain, etc. These notes do not attempt to give a complete survey of growth equations, but will be mainly concerned with one particular equation, that ascribed to von Bertalanffy (1938), which satisfies the two most important criteria — it fits most of the observed data of fish growth, and can be incorporated readily into stock assessment models.

If the length of a fish, crustacean, or lamellibranch is plotted against age, the result is usually a curve of which the slope continuously de-

creases with increasing age, and which approaches an upper asymptote parallel to the X-axis (see Figure 3.1.1). Curves of weight at age also approach an upper asymptote, but usually form an asymmetrical sigmoid, the inflexion occurring at a weight of about one third of the asymptotic weight (see Figure 3.1.2).

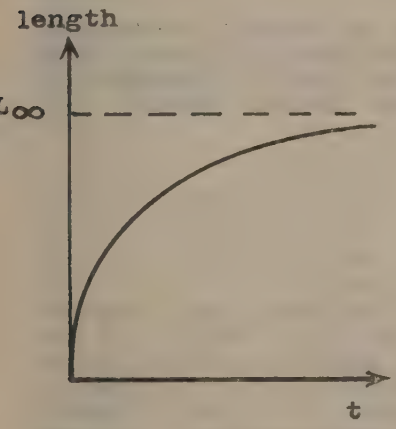

FIGURE 3.1.1. – Curve of growth by length.

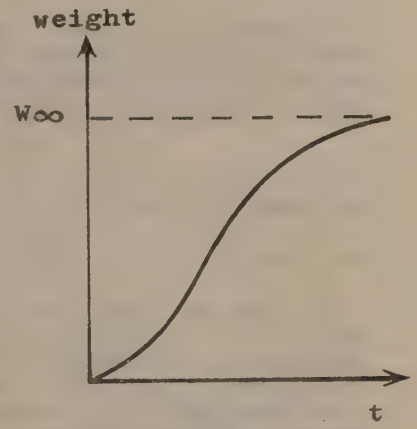

FIGURE 3.1.2. – Curve of growth by weight.

If the rate of growth in length is plotted against length, the result is often well fitted by a straight line, cutting the X-axis at a point L_∞ beyond which the fish will not grow. This is of course the asymptote of the plot of length on age. If the rate of growth in length is linearly related to length, then in mathematical terms

$$\frac{dl}{dt} = K(L_\infty - l) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (3.1)$$

where L_∞ is the value of l for which the rate of growth is zero. This equation is in the general form of a straight line relation, $y = ax + b$, with $a = -K$, $b = KL_\infty$. To integrate this differential equation, we write it in the form

$$\frac{dl}{L_\infty - l} = Kdt \text{ (see section 2)}$$

and therefore $-\log(L_\infty - l) = Kt + \text{constant}$

$$\text{or } L_\infty - l = e^{-Kt} \times \text{constant}$$

$$\text{or } l = L_\infty - \text{constant} \times e^{-Kt}$$

Putting t_o as the theoretical age at which $l = o$ we can obtain the value of the constant from the relation

$$o = L_\infty - \text{constant} \times e^{-Kt_o} \text{ or constant} = L_\infty e^{Kt_o}$$

then

$$l_t = L_\infty [1 - e^{-K(t-t_o)}] \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (3.2)$$

Equation (3.1) is identical with that deduced by von Bertalanffy (1938) on physiological grounds. He considered that growth in weight was the resultant of the difference between anabolic and katabolic factors, taken as proportional to surface area and weight respectively

$$\text{i.e.} \qquad \frac{dw}{dt} = hs - kw$$

or, putting $w \propto l^3$, $s \propto l^2$

$$\frac{dl}{dt} = H - Kl$$

In fitting the growth curve the instantaneous rate of growth will not be known, but only lengths at certain times — often one year apart when they are derived from age determination, but at irregular intervals if derived from tagging data. If the times t_1, t_2 are close together, a close approximation to the instantaneous rate of growth is given by $\frac{l_2 - l_1}{t_2 - t_1}$, where l_1, l_2 are the lengths at times t_1, t_2 respectively. If this growth rate is plotted against the mean length $\frac{1}{2}(l_1 + l_2)$, then a plot corresponding to equation (3.1) is obtained; the intercept on the X-axis gives an estimate of L_∞, and the slope an estimate of $-K$.

For data at equal time intervals of length T, from equation (3.2)

$$l_t = L_\infty [1 - e^{-K(t-t_o)}]$$

$$l_{t+T} = L_\infty [1 - e^{-K(t+T-t_o)}]$$

$$l_{t+T} - l_t = L_\infty e^{-K(t-t_o)} (1 - e^{-KT})$$

$$l_{t+T} - l_t = (L_\infty - l_t)(1 - e^{-KT}) \quad \ldots\ldots\ldots\ldots \quad (3.3)$$

The plot of increment, $l_{t+T} - l_t$, against initial length, l_t, therefore gives a line, slope $-(1 - e^{-KT})$, and an intercept, on the X-axis, of L_∞ (see Figure 3.2.1). The important special curve is $T = 1$ year, when the slope $= -(1 - e^{-K})$. An alternative form of equation (3.3) is

$$l_{t+T} = L_\infty (1 - e^{-KT}) + l_t e^{-KT} \quad \ldots\ldots\ldots\ldots (3.4)$$

which, for $T = 1$, is the well-known Ford-Walford plot, of l_{t+1} against l_t, which gives a straight line, slope e^{-K}, and an intercept on the 45° line, where $l_t = l_{t+1}$, of L_∞ (see Figure 3.2.2). This plot is essentially the

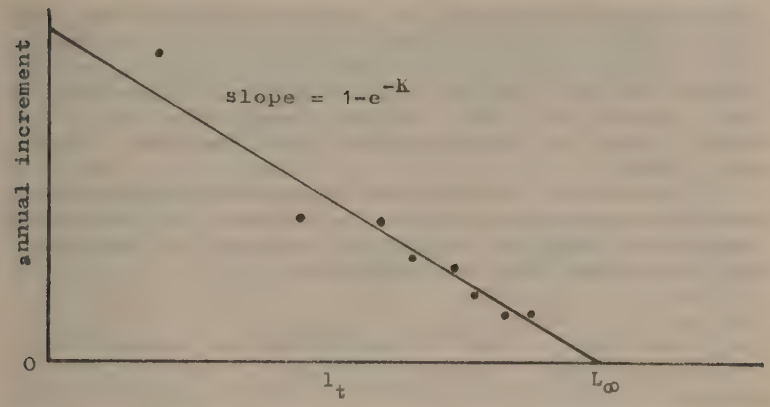

FIGURE 3.2.1. – Estimation of growth constants. Plot of length increment against initial length.

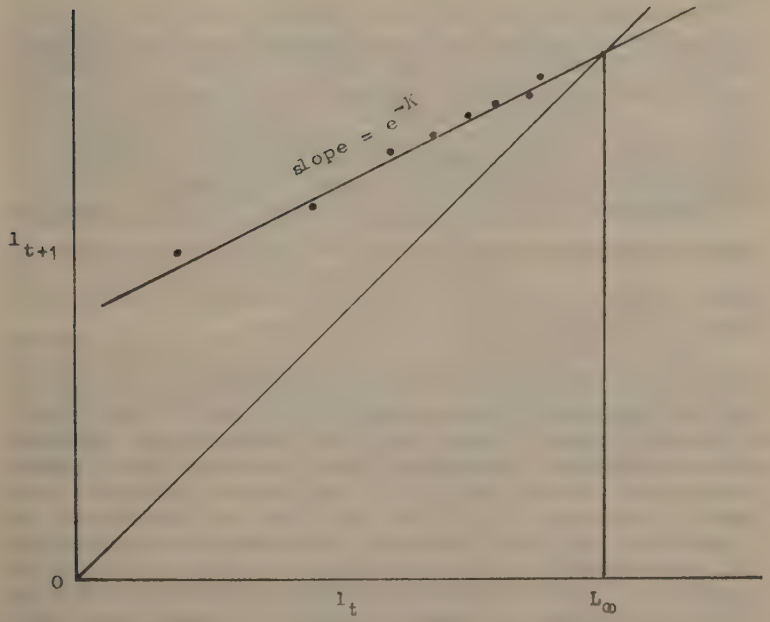

FIGURE 3.2.2. – Plot of length against length one year earlier (Ford-Walford plot).

same as the plot of increment $(l_{t+1} - l_t)$ against initial length. The points will seem to fit the Ford-Walford line better, but because the intersection of the regression line and the 45^0 line is very oblique, L_∞ is in fact estimated with equal precision by the two plots, and if the fitting is done graphically rather than by calculating regression lines, e.g. by least squares, greater errors in drawing are likely to be introduced in the plot of l_{t+1} against l_t.

L_∞ and K can be determined directly from the lines fitted to these plots either by regression analysis, or by eye; then t_o can be estimated from equation (3.2) for any particular observation of length at age. For this, equation (3.2) is best rewritten as

$$e^{-K(t-t_o)} = \frac{L_\infty - l_t}{L_\infty}$$

or

$$t_o = t + \frac{1}{K} \log_e \frac{(L_\infty - l_t)}{(L_\infty)} \quad \ldots\ldots\ldots\ldots\ldots \quad (3.5)$$

While an estimate of t_o can be thus obtained for each age for which the mean length is known, these estimates will not be equally good. Those from old fish will be highly variable, because a small difference in l_t makes a big difference to the estimate of t_o when l_t is nearly equal to L_∞, while the mean length of the youngest fish may be biased because only the bigger fish of these ages appear in the catches. The best estimate of t_o would appear to be the mean of the estimates of t_o obtained from the younger, but fully recruited, age groups.

Alternatively, only L_∞ is estimated from the plots of increment against initial length. From this $\log_e \frac{(L_\infty - l_t)}{(L_\infty)}$ can be calculated, and plotted against t. From equation (3.5) this should give a straight line, slope $-K$ intercept on the t–axis equal to t_o.

Data on length at annual intervals can be obtained and tabulated in various ways. Probably the most straightforward is the analysis of the growth of a single fish — the length at the end of each year of life being obtained from measurements along an axis of a scale, otolith or other hard structure. Alternatively, the growth of a single year–class can be followed over a period of years — i.e. for the 1956 year-class the increment in the fifth year of life is the difference between the mean length of five-year-old fish at the end of 1961 and four-year-old fish at the end of 1960. Both these methods are concerned with the growth of a group of fish during their life, the growth during each year of life providing one point in the plot. Thus the growth increments refer to different calendar years; for example for the 1956 year-class the increment in the third year of life is put on in 1959, possibly under conditions

very different to those in 1961, the fifth year of life. Growth in a particular year can be studied by taking the growth of different year-classes — e.g. data of growth in 1960 are given by the growth of the 1956 year-class in its fifth year of life, of the 1957 year-class in its fourth year of life — each year-class provides one point in the plot. This is a particularly useful method for studying the effect of the environment — food, temperature, density, etc. on growth. Finally, growth can be estimated from a single year's data, e.g. from data in 1960 the increment in the fifth year of life can be estimated from the difference in lengths of the 1955 and 1956 year-classes, the fourth year's increment from the difference between the 1956 and 1957 year-classes, etc. These differences do not, in fact, correspond to the growth of any particular fish or group of fish, and the method should be used only when other methods cannot. An improvement is to take the average size at each age over a number of years, but in this case it is usually possible, and more satisfactory, to analyse the growth of the individual year-classes or in each calendar year.

The weight of a fish is usually closely proportional to the cube of its length, so that from equation (3.2)

$$w_t = W_\infty \left[1 - e^{-K(t-t_0)}\right]^3 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (3.6)$$

where W_∞ is the asymptotic weight corresponding to the asymptotic length L_∞.

Similarly, if weight is proportional to the nth power of the length, $w_t = W_\infty (1 - e^{-K(t-t_0)})^n$.

When growth data are given in terms of weight, fitting of growth curves is most easily done by using the cube-root of the weight as an index of length, fitting this to the equations of growth in length as above, and finally cubing to return to weight.

A more general growth equation has been given by Richards (1959); with a slight change from his notation this is

$$w_t^{1-m} = W_\infty^{1-m} \left[1 - ae^{-kt}\right] \quad \ldots\ldots\ldots\ldots\ldots \quad (3.7)$$

For various values of m this equation becomes one or other of the common growth equations. Thus if $m = \frac{2}{3}$, equation (3.7) becomes the same as equation (3.2) for the von Bertalanffy curve. If $m = 2$ the equation, with some rearrangement, becomes the autocatalytic equation

$$W_t = \frac{W_\infty}{1 + be^{-kt}}$$

and for $m = 0$, the monomolecular equation

$$w_t = W_\infty (1 - ae^{-kt})$$

and it can be shown that in the limit as $m \longrightarrow 1$, the equation becomes the Gompertz $\log w_t = \log W_\infty (1 - ae^{-Kt})$. This curve satisfies a relation similar to that of equation (3.1), only in terms of log length rather than length, i.e.

$$\frac{d \log l}{dt} = K' (\log L_\infty - \log l)$$

3.2 Conversion of length to age

The expressions above give the weight or length of a fish in terms of its age. Sometimes, the inverse procedure is required, i.e. it is desired to know the age of fish of a given length, e.g. selection data are normally in terms of length, but for incorporation in yield equations need to be expressed in terms of age.

If the seasonal growth pattern is very marked, and all fish of a particular age are nearly the same length, the actual mean age of fish of a given length may be quite different from the mean age determined from the average annual growth curve, particularly at the beginning and end of the season of rapid growth. If this is the case, the conversion of length to age is best made empirically from the observed age-length curve. Also, particularly if there is much individual variation in growth, the curve of mean length at a given age will be different from the curve of mean age at a given length (just as generally the regression line of y on x is different from the regression line of x on y). Usually, however, it is sufficient to convert length to age from a growth equation fitted to all the observed data of mean length at age, e.g. the von Bertalanffy equation

$$l_t = L_\infty [1 - e^{-K(t-t_0)}]$$

To obtain t in terms of l we divide both sides by L_∞, and subtract from unity, giving

$$\frac{L_\infty - l_t}{L_\infty} = e^{-K(t-t_0)}$$

Taking natural logs of both sides gives

$$\log_e \frac{L_\infty - l_t}{L_\infty} = -K(t - t_0)$$

and therefore

$$t = \frac{1}{K} \log_e \frac{L_\infty}{L_\infty - l_t} + t_0 \quad \ldots\ldots\ldots\ldots\ldots\ldots (3.8)$$

The span of age $t_2 - t_1$ between two lengths l_1, l_2 is therefore

$$t_2 - t_1 = \frac{1}{K} \log \frac{(L_\infty - l_1)}{(L_\infty - l_2)} \quad \ldots\ldots\ldots\ldots\ldots\ldots (3.9)$$

3.3 Exercises

1. The von Bertalanffy growth equation contains three parameters (L_∞, K and t_0), which can therefore be estimated from three observations of length at age. From equation (3.2) write down the lengths at times $t - 1$, t, $t + 1$, and the increments in length between $t - 1$ and t and between t and $t + 1$. Hence determine an estimate for K from the ratio of these increments; by substituting this estimate for K in equation (3.2), or otherwise, find an estimate for L_∞, in terms of l_t and the increments.

2. Kitahama (1955) gives the following size at age data for the Pacific herring, *Clupea pallasii* C. and V., caught off the western coast of Hokkaido from 1910-54. The lengths are averages over a forty-five year period; ages determined from scale rings.

Age	Total length
years	*cm*
1	25·70
4	28·40
5	30·15
6	31·65
7	32·85
8	33·65
9	34·44
10	34·97
11	35·56
12	36·03
13	35·91
14	37·04
15	37·70

$$W = 7.8 \times 10^{-6} L^3 \text{ g}$$

(*a*) Construct a work-sheet and determine L_∞, W_∞, K and t_0.

(*b*) Calculate the theoretical curves of growth in length and weight over the range 0-15 years.

3. Yokota (1951) gives the following data for growth of the shark *Mustelus kanekonis* (age determined from seasonal changes in length of claspers).

Age	Weight
groups	*g*
I	375
II	1 519
III	2 430
IV	3 247

$$W = 7.4 \times 10^{-3} L^3 \text{ g}$$

(*a*) Determine L_∞, W_∞, K and a working value for t_o.

(*b*) Calculate curves of growth in length and weight up to age group VIII.

4. Posgay (1953) tagged sea scallops, and obtained the following data on growth during the ten months (approximately) between tagging and recapture.

	Shell diameter									
	mm									
At tagging	64	69	71	94	104	105	110	117	117	126
At recapture	98	102	93	115	120	126	125	127	136	138

(*a*) Calculate L_∞ and K.

(*b*) Taking $t_o = 0$, calculate and plot the curve of growth in length up to six years.

5. Ochiai (1956) gives the following data for the growth of the soles *Heteromycteris japonicus* and *Pardachirus pavoninus*.

Age	Standard length	
	H. japonicus	*P. pavoninus*
Years	*cm*	
1	6.09	10.00
2	8.10	14.80
3	9.20	

(*a*) Determine arithmetically L_∞, K and t_o for each species (assume $t_o = 0$ for *P. pavoninus*).

(*b*) Demonstrate the patterns of growth in weight, assuming a cubic relation of weight to length.

6. Moiseev (1946) gives the following data for growth (total length in cm) of the flatfish *Limanda aspera* in Peter the Great bay, Japan sea.

Age	Sex	Sampling year				
		1928	1930	1931	1932	1933
1	♂♀	5.15	7.60	6.58	7.72	8.34
	♀	5.77	7.22	7.20	9.50	7.34
2	♂♀	10.25	13.60	11.70	13.80	14.10
	♀	11.77	11.88	13.20	15.50	12.68
3	♂♀	16.40	19.40	17.42	18.82	19.44
	♀	17.41	19.00	18.80	21.00	18.68
4	♂♀	20.45	24.00	21.22	22.92	24.32
	♀	22.13	25.00	23.60	25.50	25.32
5	♂♀	25.05	26.80	25.42	26.38	27.66
	♀	26.51	26.12	27.60	29.50	27.32
Index of total demersal catch		1	1	5.5	8.0	7.7

(*a*) Analyse sexual differences in growth.

(*b*) Bearing in mind that large-scale fishing was started in the bay only in the season 1929-30, and that *L. aspera* formed 80 percent of the demersal catch, examine the year-to-year variation in growth. The mean age composition by number, during 1931-33, was as follows:

Age	3	4	5	6	7	8	9	10	11	12
Percent	0.6	4.7	16.1	33.3	27.9	11.3	3.4	1.7	0.9	0.2

(*c*) Estimate the total mortality coefficient and examine the growth data for bias in mean length at age, due to selection.

(This part of the exercise is to be completed after sections 5 and 7.)

SECTION 4. EFFORT AND CATCH PER UNIT EFFORT

4.1 Introduction

These two quantities may be conveniently treated together. Both provide indices related to important quantities — the fishing mortality and the density of the exploited stock. If the total catch is known (as it generally is), then if either effort or catch per unit effort is known the other can be calculated at once. Though catch per unit effort is usually a derived quantity obtained from the independent values of catch and effort, these data need not relate to an entire fishery and in practice the catch per unit is often obtained from data from some part of a whole fishery, and the total effort is estimated from it.

A distinction must be made between the use of effort data to study the stocks of fish, as described in this manual, and the use of data on the amount of fishing to study the input of the fishery in economic terms. Over a short period both may be measured by the same set of figures, say days at sea, but if there are technical improvements in the fishery then the statistics of the amount of fishing should be adjusted in different ways. For instance, suppose the introduction of sonar equipment doubles the fishing power, and hence on the average doubles the catch per day of a purse-seiner. Then to the biologist the effort exerted per day fishing has doubled, and the statistics of days fishing should be adjusted accordingly; to the economist the input is increased only slightly, to allow for the cost of the sonar equipment.

Though the catch per unit effort will rarely be exactly proportional to the stock density, it is often essential to have some measure of the stock, and the catch per unit will nearly always be the best available — better than for example, total catch. As research into the fishery develops, requiring better indices of stock magnitude so, in general will the measure of catch per effort become better, being refined by taking into account the spatial distribution of fishing, differences in the fishing power of vessels, etc.

In some situations a satisfactory measure of stock density (and hence an index of catch per unit effort) can be obtained quite independently of catch and effort data. This index can then be used, by dividing into the figure of the total catch, to provide an index of total effort. For instance, recent developments in surveying techniques using sonar and echo-sounding suggest that for some pelagic fisheries, in which normal catch and effort data are often difficult to interpret, the most re-

liable index of density will be derived from echo- or sonar-survey data, expressed say, as so much trace per mile steamed. The corresponding index of effort is then the catch divided by the index of density, i.e. tons caught per unit trace.

4.2 The mathematical formulation

The relations between catch, effort and stock density are clear for the operations of a single unit on a uniform density of fish, e.g. a trawl which may be considered as taking at each haul a fixed proportion of the fish present. Then the catch per operation is proportional to the stock density, and the number of operations is proportional to the mortality caused.

Mathematically, if the catch of one operation is proportional to the stock density

$$\Delta C = q \,.\, \Delta f \,.\, N/A \quad \ldots\ldots\ldots\ldots\ldots\ldots (4.1)$$

where ΔC = catch of one operation

q = constant

Δf = fishing effort exerted by unit operation

N = mean stock abundance

A = area inhabited by the stock

The catch, in numbers, is equal to the number of deaths due to fishing, which, in the following section, will be shown to be written conveniently in terms of instantaneous rates

$$\left[\frac{dN}{dt}\right] \text{fishing} = -FN$$

where F = fishing mortality coefficient

or, in terms of short intervals

$$\Delta C = -(\Delta N) \text{ fishing} = FN\,\Delta t$$

Therefore,

$$q\,\Delta f \,.\, N/A = FN\,\Delta t \quad \ldots\ldots\ldots\ldots\ldots\ldots (4.2)$$

and

$$F = q \frac{\Delta f}{A \Delta t}$$

i.e., the fishing mortality coefficient is proportional to the fishing intensity, where the fishing intensity is defined as the fishing effort per unit area, per unit time.

This may be written

$$F \Delta t = q \cdot \frac{1}{A} \Delta f$$

and if q and A are constant, adding up over a period length t

$$Ft = q \cdot \frac{1}{A} \cdot f$$

where f is the total fishing effort during the period or

$$F = q \cdot f/At \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (4.3)$$

$$= q \times \text{fishing intensity}$$

In practice A, the area inhabited by the stock will be constant, and over a fixed time period, say one year, we can write

$$F = q' f \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (4.4)$$

where q' = constant, and this is the form in which the relation between fishing mortality and fishing effort is usually expressed.

The basic equation (4.1) for the single operation can be written in terms of catch per unit effort

$$\frac{\Delta C}{\Delta f} = \frac{q}{A} \cdot N = qD$$

or, again assuming q and A are constant, averaging over a period

$$C/f = q/A\bar{N} = q\bar{D} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (4.5)$$

where $\bar{N}$, $\bar{D}$ are the average abundance and density during the period. Therefore catch per unit effort is proportional to the density, but again, if A is constant then catch per unit effort will also be proportional to the abundance.

These calculations, which express for all the operations during some period the fishing effort as an index of mortality or the catch per unit effort as an index of density, require that all the operations are expressed in standard units, i.e. that the constant q in equation (4.1) should be the same for all operations. A simple form of operation is a day at

sea of a single boat, so that a simple measure of effort is the number of days at sea, and of catch per unit effort, the catch per day at sea. In attempting to improve this simple measure, we are concerned with how, during an average day at sea a greater or lesser proportion of the stock can be caught. As usual, small short-term fluctuations are generally irrelevant for the purposes of this manual, the important factors being those causing long-term trends.

The catch per day at sea of a ship can be increased for a given stock density:

(*a*) Because during actual fishing time more fish are caught (the fishing power of the ship is increased).

(*b*) Because more actual fishing time is spent per day; in addition, since the distribution of a stock is never completely uniform, but there are local concentrations of higher density than the average, another possibility is

(*c*) Because the ship operates in local areas of greater density.

Standardization of fishing effort data therefore depends on determining whether there are appreciable variations (especially trends) in effective fishing time, fishing power, or distribution of the fleet, and if so making the necessary standardization of the appropriate component of the total fishing effort. The precise method of standardization is best determined after the changes, or likely changes have been identified. For instance, for trawlers it is well known that the fishing power increases with both size (tonnage) and horsepower. If the composition of a trawler fleet does not change, even though there are both large and small vessels, then there is no immediate need to standardize. But if there are changes, and the average sizes, or power of the ships increase, then some standardization must be done. If the change is a matter of new ships being built which are both bigger and more powerful, then the standardization might be in terms either of tonnage, or horsepower (or possibly some other index of size or power) whichever is most convenient. If the changes are a matter of putting bigger engines into existing vessels, then standardization must be in terms of horsepower (or other index of engine size).

4.3 Fishing time

Standardization of fishing time may be approached by subtracting from the basic data of days at sea the periods which are not directly occupied with catching or locating fish. These include:

(*a*) Time lost through bad weather.

(*b*) Time steaming to and from the fishing grounds.

(*c*) Time during which the gear is being prepared for fishing, but is not actually in operation.

(*d*) Time spent handling the catch, after it has been caught.

The proportions that these elements of the nonproductive time form of the total time at sea will vary for various reasons. Bad weather may be expected to fluctuate randomly, and may often be ignored, but bigger or better designed vessels may be able to fish in worse conditions and therefore lose less time.

Steaming time will be reduced by the use of faster vessels, but may increase as the nearer grounds are depleted, and the ships have to go further afield (in this case catch per day on the grounds might provide the better index of fish density on the grounds fished, but catch per day at sea a better index of general stock abundance).

Changes in the time lost handling the gear or the catch may be important, especially when correlated with stock abundance. At high levels of stock much time may be lost handling the catch, or in making only short trawl hauls (with proportionately much less time with the gear on the bottom), so that changes in the catch per day on the grounds (or day fishing) will tend to underestimate changes in the stock density.

The productive time will include:

(*a*) Time on the fishing grounds, searching for fish, and

(*b*) Time when the gear is in operation, catching fish.

The relative importance of these two aspects of fishing time will depend on the type of gear. At one extreme is whaling, where the gear (harpoon) is only in operation for a very short time, and the important measure is the time spent searching for whales. At the other extreme, bottom trawlers spend little time searching and the important measure is the time for which the gear is on the bottom, catching fish. For some gear, e.g. purse-seines, it may not be clear which measure, fishing time or searching time, or combination of both, should be used, and for these gears it may be best to take as the basic unit of fishing time the time on the grounds (expressed as days or hours). Such statistics should then be supplemented by detailed log-book records (possibly for only a sample of the fleet) on how the total time on the grounds is spent — searching, preparing the gear, actual catching, handling the catch — with the expectation that later analysis and a fuller understanding of how the fishery operates may help to derive a better index of fishing time.

For some gear, e.g. long-lines, gill-nets, which, like trawls, catch more or less continuously, the efficiency of operations changes with changing duration of the operation. Thus a long-line set for twelve hours may catch more than one set for six hours, but not twice as much. This effect may be considered as a change in fishing power, or

in effective fishing time, but the relevant information is best collected in terms of fishing time. If the average duration of set is unchanged, the effect may not be important, though in some fisheries the extent of the effect depends on the abundance of the stock; thus an extreme example is a scallop dredge, which may in some fisheries fill up and cease to catch any more after perhaps twenty minutes, even though towing is continued for half an hour or more. Fishing time for such gears is then best collected in a convenient form (say number of sets), and an adjustment made for any change in the average duration of set, or for any effect of gear saturation.

4.4 Fishing power

The fishing power of a particular gear, i.e. the catch it takes from a given density of fish per unit fishing time (in the units of fishing time appropriate to that gear), can be thought of in two parts

(*a*) The extent (area or volume of water) over which the influence of the gear extends, and within which fish are liable to be caught (= a say).

(*b*) The proportion of the fish within this area which are in fact caught (= p say).

Clearly if fish or fishing were randomly distributed, then the proportion of the total stock within the area of influence would be $^{a}/_{A}$, and the catch would be $^{a}/_{A} \times N$. That is, the product $p \times {}^{a}/_{A}$ would give a direct measure of the fishing mortality (see section 5.3).

Improvements to fishing techniques can affect either quantity. For instance, for purse-seiners the area of influence can be increased by better searching — faster ships, use of advanced detection equipment etc. — while the proportion of the population in this area that can be taken may be increased by the use of a larger net, or by some of the sonar equipment.

Changes in fishing power are least important in stationary gears, traps, lines, etc., where the basic unit of gear — the single lobster pot, or the baited hook — does not change much, and the fishing power of the individual vessel is increased by carrying more pots, or using more hooks. The effort can therefore be readily expressed in standard terms as number of pots, or number of hooks, etc. multiplied by a suitable measure of fishing time (which will often be one operation, adjusted if necessary to a standard duration of operation).

The fishing power of the more active gears — trawls, purse-seiners, etc. — are more likely to change with improvements in the vessel or gear. For instance the average size of United Kingdom trawlers fishing at Iceland has almost doubled during the past thirty years, and prob-

ably also the size of net has increased, though the data on the details of the gear used are not as good as the vessel data. In this fishery, and in some other trawl fisheries analysed in detail, the fishing power has been shown to be closely proportional to the gross tonnage of the trawler or to the horse power of the engine. Tonnage or horse power is therefore a convenient index of fishing power, and fishing effort data may be expressed in standard terms such as ton-hours (i.e. hours fishing times average tonnage of the vessels).

For purse-seiners also large vessels catch more than small vessels, but the catch goes up less than proportionately to tonnage. Thus for the United States tuna fishery in the eastern Pacific correction factors have been used for each size category of vessel to adjust their effort to that of vessels between 100 and 200 tons; these factors ranged from 0.60 for vessels less than 50 tons to 1.37 for vessels over 200 tons.

For this type of gear, it is best, if there have been appreciable changes in the fleet during the period of study, to take one vessel, or group of vessels as standard, and determine from catch records the fishing power of other vessels, or group of vessels, relative to the standard vessel. The fishing effort for the fleet as a whole can then be expressed in standard terms.

4.5 Distribution of fishing

When the fishing power and fishing time have been fully standardized, the resulting catch per unit effort will be proportional to the average density at the positions fished, the average being weighted according to the amount of fishing at each place. This average density will almost certainly be greater than the true average density, because most fishing will be done on the grounds giving good catches. The catch per unit effort will, however, still be a valid index of the density so long as the ratio of the true density to the density weighted by the amount of fishing remains constant. The difference between the true average density and the average density taken over the positions fished may be considered in two parts, corresponding to fishing tactics — getting the best catch on a particular ground — and fishing strategy — making the best choice of grounds taking into account such things as different steaming time to different grounds, the different species composition on the grounds, and the different prices for different species, etc. On any given fishing ground, which for the North sea trawl fisheries may be thought of as say ten miles across, the distribution of fishing will be determined solely by the fishermen's ability to find the small local concentrations of fish. The density in the unfished parts of the fishing ground will be unknown, but the ratio of the density in the fished areas to the average density will generally be constant, at least over a short period. Over a longer period the introduction of new devices may permit the fishermen to

concentrate more effectively on the fish, either directly (echo sounding) or by more accurate navigation (e.g. Decca, radar or echo sounding). These improvements may be most easily considered and analysed as changes in the fishing power of the fishing unit (vessel, plus fishing gear plus other gear). To the first approximation, though, we may write, for any one fishing ground, from equation (4.5)

$$\frac{C}{f} = q^1 \tilde{D} = qD \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (4.6)$$

where C = catch, f = effort

q, q^1 are constants

and $\tilde{D}$ = density, weighted by amount of fishing

D = true average density on that ground

A unit stock will usually be distributed over several fishing grounds and the ratio of total catch to total effort will be equal to the weighted mean of the catches per unit effort in the various grounds, weighted by the effort on each ground, i.e.

$$\frac{C}{f} = \frac{\Sigma\left[\frac{C_i}{f_i} \times f_i\right]}{\Sigma f_i}$$

where C, f are the total catch and effort, and C_i, f_i the catch and effort in a particular fishing ground.

Since the distribution of fishing is likely to vary from year to year due to changes in the relative abundance of different stocks, etc., these weighting factors will vary, and the ratio of the total catch per unit effort to stock abundance will also vary (unless the density of fish on all grounds is the same).

However, from equation (4.6) we can for any fishing ground, i, whose area is A_i say, express the number of fish as

$$N_i = A_i D_i = \frac{A_i}{q_i} \times \frac{C_i}{f_i}$$

If the whole range of the stock can be subdivided into regions, within each of which equation (4.6) can be applied, then by adding, the total number in the stock is

$$N = \Sigma_i N_i = \Sigma \left[\frac{A_i}{q_i} \times \frac{C_i}{f_i} \right]$$

If q_i is constant $= q$ for all grounds, then

$$N = \frac{1}{q} \Sigma \left[A_i \times \frac{C_i}{f_i} \right]$$

$$\text{and density} = D = \frac{N}{A} = \frac{1}{q} \times \frac{1}{A} \times \Sigma \left[A_i \times \frac{C_i}{f_i} \right] \quad \ldots\ldots \quad (4.7)$$

where

$$A = \Sigma A_i ;$$

i.e. the density is the weighted mean of the catches per unit effort in each subregion, the weighting factors being the areas of the regions. If all the areas are of equal size, this reduces to

$$D = \frac{1}{nq} \Sigma \frac{C_i}{f_i} \text{ where } n = \text{number of areas}$$

The effective total effort (that is, the measure of effort which will remain proportional to the fishing mortality regardless of changes in the distribution of fish and fishing) can be derived from equation (4.7) by dividing into the total catch, i.e.

$$f = \frac{C}{qD} = A \Sigma C_i \div \Sigma \frac{A_i C_i}{f_i}$$

These formulae also allow density indices to be obtained for any particular subgroup of the population, e.g. an age group. If the density index for the entire population is given by total catch divided by total effort, then the index for a given age group is found by dividing the number landed of that age group (see section on sampling) by the total effort. Otherwise the index is obtained by raising the number of each age in a unit weight by the weight caught per unit effort. If there are marked differences in composition between different regions of the stock then the density indices will have to be obtained for each region separately, and the index for the whole stock obtained by weighting up by

the areas of each region. The size of these regions should be small enough to ensure uniform composition within them, but in general should be larger than the separate grounds, which, as discussed earlier, are used in giving the overall density index.

The analysis of catch and effort data by small areas is particularly valuable when more than one species is being exploited, each species living in slightly different, but perhaps overlapping, parts of the whole fishing region. The proportion of a given species in the catch will therefore, depend as much on where the catch was made, as on the abundance of that species. Within a sufficiently small subarea, however, the proportion of a given species in the catch will be more nearly constant, and unaffected by the precise fishing position.

Another method of analysing fishing effort data on mixed species is possible when any one landing can be allocated according to the species which was the main objective of that trip — for example German trawlers fishing at west Greenland land during the year roughly equal quantities of cod and redfish, any one landing however usually consists predominantly of cod or of redfish. The stock density of cod will then be estimated from the catch per unit effort of those trawlers fishing specifically for cod, and the density of redfish from the catches of those fishing for redfish. (Another method is discussed by Ketchen in International Council for the Exploration of the Sea, 1964 b.)

4.6 Several gears

When more than one group of vessels is exploiting a unit stock — e.g. otter trawlers and longliners, or vessels from several countries — it will usually be difficult or impossible to express the effort statistics from all vessels in the same units, and thus to obtain directly a figure for total effort. One single fleet (A) may therefore be taken as standard, and its catch per unit effort taken as the best index of density, and total effort estimated as

$$\text{Total effort} = \text{Effort of fleet (A)} \times \frac{\text{Total catch}}{\text{Catch of fleet (A)}} = \frac{\text{Total catch}}{\text{Catch per unit effort of fleet (A)}}$$

If reasonable effort statistics are available from more than one fleet it is best first to calculate catch per unit effort figures for each fleet separately, and then compare the year-to-year changes in the indices of abundance thus obtained. If each separate index follows much the same trend, then this is some confirmation that each is a fair measure of the abundance (the degree of confirmation increases with the diversity of the fleets concerned, e.g. it is more encouraging if data from trawlers

and long-liners agree, than if two trawl fleets agree). Conversely, if there is a discrepancy between two sets of catch per unit effort figures, then one, and possibly both, is not a good measure of abundance. Before using either set of data the methods of obtaining them must be examined to see where the discrepancy might arise (e.g. one fleet has included an increasing number of new and powerful vessels, not taken account of in the effort statistics used). If two or more fleets give consistent indices of catch per unit effort, then a single pooled index of catch per unit effort (and hence of total effort) can be conveniently obtained by expressing the index for each fleet as a percentage of some standard year, or period of years.

4.7 Exercises

1. Outline briefly the types of gear used in fisheries with which you are familiar.

2. What measures of effort are at present available?

3. What measures of effort would, ideally, be the best to use?

4. What are the possible causes of differences in fishing power, or fishing effort, between vessels or groups of vessels comprising the fleet?

5. Are there any reasons to suppose that, in any of these fisheries, the catch per unit effort is not proportional to the stock abundance; if so, can this lack of proportionality be overcome by using a better measure of effort?

6. The table below is an extreme simplification of United Kingdom North sea trawl data and represents the effort and catches of plaice and haddock in two years. The area has been divided into sixteen subareas in each of which the data of catch and effort have been recorded separately.

(*a*) For each year obtain, by addition, total catch of each species and the total effort, and hence calculate the ratio total catch/total effort.

(*b*) Draw up a chart for each year showing the catch per unit effort of each species in each rectangle.

(*c*) Calculate for each species an overall density index, i.e. the mean catch per unit effort, and the effective fishing intensity on each species each year.

Compare the fishing intensities on the two species.

	Year 1				Year 2			
Effort	5	6	6	3	16	17	13	14
Haddock	50	48	60	24	208	238	195	168
Plaice	0	12	6	0	0	17	13	0
Effort	8	7	9	8	13	12	13	10
Haddock	40	49	54	48	130	132	91	80
Plaice	16	0	27	8	13	12	26	0
Effort	10	13	11	14	9	9	(8)	6
Haddock	40	65	33	56	45	63	(32)	48
Plaice	40	39	22	42	18	18	(8)	18
Effort	14	15	16	15	5	5	6	4
Haddock	28	0	16	15	10	5	6	4
Plaice	84	90	48	45	25	15	12	8

Compare the change in density between the two years as measured by the ratio total catch/total effort, and by mean catch per unit effort.

(*d*) Supposing that there had been no fishing in the second year in one of the middle rectangles, as indicated by brackets in the table, how could mean density or effective overall fishing intensity be calculated? Make some reasonable assumption as to the density in the subarea; try the effect of different assumptions. Some assumptions are: that the density is the mean of surrounding subareas; that the change from the previous year is the same as that for other subareas; (as a limiting case) that the density is zero.

7. The table below gives the catch and effort statistics for the cod fishery in the International Council for the Exploration of the Sea Region I (Barents sea). The catches are given in tons (the total includes German and Norwegian catches), United Kingdom fishing effort as millions of ton-hours (hours fishing × mean tonnage of the fishing vessels), and U.S.S.R. fishing effort as thousands of hours fishing.

Calculate the catch per unit effort of the United Kingdom and U.S.S.R. fleets.

Calculate the total fishing effort in United Kingdom and in U.S.S.R. units.

Year	Catch			Effort	
	United Kingdom	U.S.S.R.	Total	United Kingdom	U.S.S.R.
1946	53 835	117 100	199 640	17.6	104
1947	127 242	151 970	340 758	38.4	149
1948	164 794	158 650	406 620	63.1	162
1949	226 450	162 340	484 942	80.0	171
1950	136 790	135 410	356 474	93.2	161
1951	129 030	189 580	407 989	98.9	231
1952	130 546	258 830	524 160	102.6	247
1953	59 445	261 400	442 839	53.1	275
1954	72 347	404 650	597 534	51.5	340
1955	91 379	530 280	830 694	60.6	373
1956	67 787	512 170	787 070	54.3	492
1957	38 488	183 000	399 595	44.5	—
1958	46 225	146 570	388 067	55.6	—

For each fleet express the annual catch per unit effort as a percentage of the 1946-56 average; are the trends in the two series the same? Might the difference be accounted for by the fact that one series contains a factor (tonnage) which makes some allowance for increased fishing power of the individual trawlers?

8. German trawlers fish at west Greenland for both cod and redfish. Their catches in tons and fishing efforts during 1958 and 1959 were as follows (data taken from *Statistical bulletins* of the International Commission for the Northwest Atlantic Fisheries).

Year	Primary species	Days fished	Catch of cod	Catch of redfish
1958	Cod	1 337	26 247	1 754
	Redfish	385	1 277	9 457
	Mixed	199	2 386	1 969
	Total	1 921	29 910	13 180
1959	Cod	645	12 336	1 087
	Redfish	690	2 705	15 683
	Mixed	169	2 372	2 062
	Total	1 504	17 413	18 832

Estimate, from the catch per unit effort of cod by the trawlers fishing for cod, and of redfish by trawlers fishing for redfish, the changes (as percentages) in the densities of the stocks of cod and redfish between 1958 and 1959. Compare these with the changes in the catches per unit effort of cod and redfish by all vessels taken together, and also with the changes in the catches per unit effort of cod by the redfish vessels, and of redfish by the cod vessels.

SECTION 5. MORTALITIES

5.1 Introduction

When studying mortalities we are concerned with rates of change, and it is generally most convenient to deal with instantaneous rates of change (see section 1); that is, the rate at which the numbers in the population are decreasing can be written as

$$\frac{dN}{dt} = -ZN$$

where Z is defined as the instantaneous total mortality coefficient. From this equation the number N_t alive at any time will be given by (see section 2.4.1, exercise No. 18).

$$N_t = N_o e^{-Zt}$$

where N_o = number alive at time $= o$.

Often we are concerned with considering separately two causes of removal from the population — natural deaths (disease, predation, etc.) and fish caught; then we can write

$$\left(\frac{dN}{dt}\right)\text{natural} = -MN$$

where M = natural mortality coefficient

$$\left(\frac{dN}{dt}\right)\text{fishing} = -FN$$

where F = fishing mortality coefficient

then in a very short time interval dt, the deaths due to fishing will be equal to $FNdt$, natural deaths $MNdt$, and total deaths $ZNdt$, therefore

$$F + M = Z$$

i.e. instantaneous mortality coefficients are additive.

5.2 Estimation of total mortality

Before estimating the fishing and natural mortalities separately, it is convenient to estimate the total mortality. This is readily done if we know the abundances, say N_o, N_1 of any group of fish at two known times, for then the fraction surviving is $\frac{N_1}{N_o} = S$, and the total mortality coefficient is given by

$$e^{-Zt} = S = \frac{N_1}{N_o} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (5.1)$$

or

$$Zt = -\log \frac{N_1}{N_o} = \log \frac{N_o}{N_1} \text{ where } t = \text{interval of time}$$

This has the obvious special case where $t =$ one year. The same formulae also hold when the true abundances are not known, but indices of them, e.g. catches per unit effort, are available, i.e. number n_o, n_1 proportional to N_o, N_1 then

$$\frac{n_1}{n_o} = \frac{N_1}{N_o} = S$$

Often abundances, or indices of abundance, will not be known at any particular exact time, but only as averages over finite periods of time, e.g. a year. In terms of the abundance at the beginning of the period, N, and the total mortality coefficient, Z, the average abundance during the period, duration T, may be denoted by $\bar{N}$; the numbers alive at time t are Ne^{-Zt} so that

$$\bar{N} = \frac{1}{T} \int_o^T Ne^{-Zt}\, dt = \frac{N}{ZT}(1 - e^{-ZT})$$

If we denote by appropriate suffixes the values of numbers and mortalities during periods 0 and 1, of duration T, starting a year apart we have

$$\bar{N}_o = \frac{N_o}{Z_o T}(1 - e^{-Z_o T})$$

$$\bar{N}_1 = \frac{N_1}{Z_1 T}(1 - e^{-Z_1 T})$$

and also $N_1 = N_o e^{-Z_o}$

Taking the ratio of the average abundances, we have

$$\frac{\bar{N}_1}{\bar{N}_0} = \frac{N_1}{Z_1}(1 - e^{-Z_1 T}) \Big/ \frac{N_0}{Z_0}(1 - e^{-Z_0 T})$$

$$\text{i.e. } \frac{\bar{N}_1}{\bar{N}_0} = e^{-Z_0} \times \frac{Z_0}{Z_1} \times \frac{(1 - e^{-Z_1 T})}{(1 - e^{-Z_0 T})} \quad \ldots\ldots\ldots\ldots\ldots \quad (5.2)$$

If $Z_0 = Z_1 = Z$, then equation (5.2) reduces to

$$\frac{\bar{N}_1}{\bar{N}_0} = e^{-Z}; \quad \text{or} \quad Z = \log_e \frac{\bar{N}_0}{\bar{N}_1}$$

i.e. the ratio of the mean abundance can be used in the same manner as the ratio of instantaneous abundances in equation (5.1).

The simplification can also be made if $Z_0 T$ and $Z_1 T$ are both small, even if not equal, for then $1 - e^{-Z_1 T}$ is nearly equal to $Z_1 T$ and similarly for $1 - e^{-Z_0 T}$. The last two factors in equation (5.2) then cancel out, and equation (5.2) becomes $\frac{\bar{N}_1}{\bar{N}_0} = e^{-Z_0}$. The ratio of the mean abundances during two periods therefore provides a good estimate of the survival during the year if either the mortality is constant, or the change in numbers during both periods is small. Even if these conditions are not satisfied, the ratio may still provide a fair first approximation, subject to corrections which may be deduced from equation (5.2).

The formulae above will usually be applied to the abundances of individual year-classes and enable estimates to be made of the mortalities between any pair of successive years and for any fully recruited year-class. These estimates are likely to be quite numerous, and the question then arises as to how the "best" combined estimate of mortality can be obtained. A single combined estimate is only valid if there are no systematic differences in mortality, either with age or time, over the period considered; these may be most easily detected from an array such as Table 5.1, either by inspection of the means of rows and columns, or more rigorously by a statistical test, such as the analysis of variance.

The entries in such a table should always be in the form of instantaneous coefficients, not percentage mortalities, as it is easy to show that the latter are biased, being underestimated by an average amount depending on the variance of the data, and that this bias may be quite appreciable when taking the mean of several estimates. This bias is

TABLE 5.1. – HYPOTHETICAL EXAMPLE OF ESTIMATED TOTAL INSTANTANEOUS MORTALITY COEFFICIENTS FOR DIFFERENT PAIRS OF YEAR AND AGE GROUPS

Year \ Age	4/5	5/6	6/7	7/8	8/9	9+/10+	Mean
1950/51	0.75	0.80	0.65	0.70	0.55	0.75	0.70
1951/52	0.70	0.80	0.75	0.60	0.65	0.55	0.68
1952/53	0.65	0.60	0.85	0.70	0.85	0.70	0.72
1953/54	0.70	0.75	0.65	0.90	0.50	0.50	0.67
Mean	0.70	0.74	0.72	0.72	0.64	0.62	0.69

due to the numerator in equation (5.1) being not known exactly; the overestimate of the survival when the numerator is too low is greater than the underestimate when the numerator is, to the same extent, too high. A similar bias may be seen in comparing the mean of the reciprocals of a set of numbers, which is not the same as the reciprocal of their mean.

If there are no appreciable systematic differences between years or ages, then the entries in Table 5.1 can be considered as separate estimates of the same true mortality, and the combined estimate with least variance will be given by taking the weighted mean, with weights inversely proportional to the variances of the individual estimates. These variances will generally be unknown and though obviously the variance for the very old and scarce age groups will be high, the present evidence (on limited data for plaice, herring and haddock) suggests that the variance is about constant for all the well-represented age groups (from four to eleven years for the North sea plaice). Thus, if the data for the older groups are combined (e.g. the last column of Table 5.1), all the variances will be nearly equal, and the appropriate overall estimate will be the simple mean of all the individual estimates. The mean estimate for the mortality between any one pair of age groups in all years may be determined in the same way, i.e. taking the simple mean of the estimates of Z for each pair of years, or taking the weighted mean, giving greater weight to those years for which the variance of Z is likely to be small (e.g. years in which more samples were taken). Another common method for estimating the mortality between successive years is to take the decrease in the total numbers of all fully exploited year-classes, the ratio of four years and older to five years and older. This is effectively weighting the estimates in Table 5.1 by the numbers of fish at each age.

The effect of using poor figures for effort and catch per unit effort, such that the latter does not bear a constant ratio to the true abundance, may be deduced from equation (5.1). Suppose the relation between

catch per unit effort and abundance in the two years is given, with the obvious notation, by

$$n_1 = \frac{C_1}{g_1} = q_1 \bar{N}_1 ; \quad n_2 = \frac{C_2}{g_2} = q_2 \bar{N}_2$$

Then

$$\frac{n_2}{n_1} = \frac{q_2 \bar{N}_2}{q_1 \bar{N}_1}$$

and

$$\bar{N}_1 = N_1 \left(\frac{1 - e^{-Z}}{Z} \right)$$

$$\bar{N}_2 = N_2 \left(\frac{1 - e^{-Z}}{Z} \right) = N_1 e^{-Z} \left(\frac{1 - e^{-Z}}{Z} \right),$$

then

$$\log_e \frac{n_1}{n_2} = \log_e \frac{q_1}{q_2} + Z \quad \ldots\ldots\ldots\ldots\ldots \quad (5.3)$$

Thus the estimated mortalities will include an extra term, equal to the logarithm of the change in q (the " availability " or " catchability coefficient "). A change in q will show, in an array such as Table 5.1, as a year-to-year change in mortality unconnected with changes in fishing or other causes of mortality.

Changes in availability are particularly likely to cause serious errors when there is any trend in the values of q. This may be unlikely when using annual figures, but it is often tempting to use the decline in catch per unit effort (either of a single age group or of the stock as a whole) during part of the year to provide an estimate of mortality. Nearly all fisheries show more or less pronounced seasonal changes in catch per unit effort, but while in some fisheries the fluctuations in catches per unit effort may follow precisely the fluctuations in abundance — the increases being due to recruitment and growth, and the decreases due solely to mortality — very often the major causes of the fluctuations are " availability " changes, with the fish being particularly vulnerable to capture at certain seasons, e.g. when concentrated for spawning (similar fluctuations over a 24-hour cycle may often be observed, when there is no question that the decrease during, say, daylight, is due to the stock abundance really being lower).

As a general rule, therefore, short-term changes in catch per unit effort should not be used in estimating mortalities. Normally mortalities will be estimated from mean annual values, or from periods twelve months apart. Special techniques may be necessary to estimate indices of abundance and hence mortalities, for highly seasonal fisheries where

the precise timing of the peak of the season may be different in different years.

Data on the abundance of successive year-classes at any one time can be used in a similar way as data on the abundance of the same year-classes in successive years. Taking t_c as the age at which fish enter the fishery, at which time the numbers of two successive year-classes are N_o, N_o', then their abundances at the time when they are aged $t+1$ and t will be

$$N_{t+1} = N_o\, e^{-Z(t+1-t_c)}$$

$$N_t = N_o'\, e^{-Z(t-t_c)}$$

$$\therefore \log_e \frac{N_t}{N_{t+1}} = \log \frac{N_o'}{N_o} + Z \quad \ldots\ldots\ldots\ldots \quad (5.4)$$

Catch per unit effort, or even percentage age data, can be used as indices of abundance directly in the equation, for the coefficient q, related to availability, in the top and bottom of the ratio, relates to the same period, and therefore cancels out, namely

$$\log_e \frac{n_t}{n_{t+1}} = \log_e \frac{qN_t}{qN_{t+1}} = \log \frac{N_o'}{N_o} + Z \quad \ldots\ldots\ldots \quad (5.5)$$

Equations (5.3) and (5.5) are very similar, both containing a term additional to the true mortality. Ratios of catch per unit effort of the same year-class, i.e. equation (5.3), are best to use when year-class strength is variable, or when " availability " changes are small and effort is readily measured. Equation (5.5) is better when measurement of effort is difficult, or year-class variation is small, and also when data are available only for isolated years. A disadvantage of equation (5.5) is that it does not measure the contemporary situation — the additional mortality undergone by the older of two adjacent age groups is that which it underwent during its first year in the fishery and later mortalities have been applied to both year-classes equally. Thus if fish recruit to the fishery at three years old, the ratio of six- to seven-year-old fish in the 1965 catches provides a measure of the mortality in 1961 (the year before the fish, now six years old, recruited to the fishery).

Estimates of total mortality over a period can also be obtained by semigraphical methods. If Z (the total mortality) is constant we can give the numbers of a year-class at any time, t, after it is subject to the full mortality, as

$$N_t = N_o e^{-Zt}$$

where

N_o = numbers at time $t = o$

therefore

$$\log_e N_t = \log_e N_o - Zt .$$

If now $\log_e N_t$ is plotted against t, it will give a straight line of slope $-Z$. This plot can be made either for the catch per unit of a single year-class at different times, in which case deviations (other than sampling variance) will be caused by changes in "availability," or for numbers of different year-classes at the same time — the well-known "catch-curve." (A detailed analysis of such curves, including the interpretation of nonlinear catch-curves is given by Ricker, 1958.) Deviations will be caused in the catch-curve by inequalities in original year-class strength, but the value of the "availability" in the year of sampling will alter only the position of the curve, and not its slope, or the scatter of the points. This graphical method can also (and probably most easily) be used by plotting N_t against t on semilogarithmic paper. This should give a straight line, from which the mortality is best estimated as follows. Note where the line has some convenient value (say 100), find the value on the line exactly one year later (equals say 65). Then the survival through one year $= \frac{65}{100} = e^{-Z}$ from which Z can be at once looked up in suitable tables (see Figure 5.1).

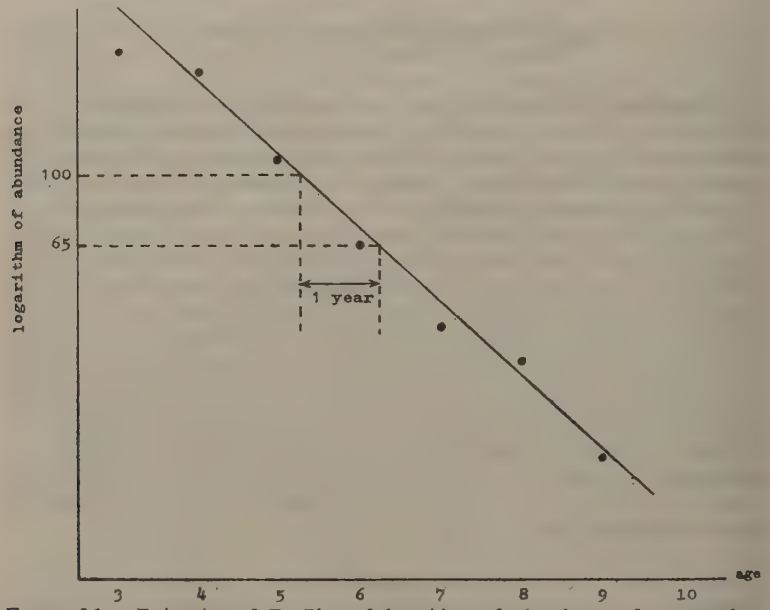

FIGURE 5.1. – Estimation of Z. Plot of logarithm of abundance of a year-class against age.

All the above methods, when applied to age composition of catches, are subject to bias when the different ages are not equally vulnerable to the gear used. If the vulnerabilities of successive ages, t, $t+1$ are ${}_tq$, ${}_{t+1}q$, the catches, or catches per unit effort, are given by

$$n_t = {}_tq \cdot N_t$$

$$n_{t+1} = {}_{t+1}q \cdot N_{t+1}$$

$$\log_e \frac{n_t}{n_{t+1}} = \log_e \frac{{}_tq}{{}_{t+1}q} + \log_e \frac{N_t}{N_{t+1}}$$

$$= \log_e \frac{{}_tq}{{}_{t+1}q} + Z$$

In practice this type of bias may be difficult to detect, unless there are abrupt changes with age, when the apparent mortality will also change with age, though the possibility of its existence should never be neglected. Because such differential vulnerability by age implies that fishing mortality is different for each age, the forms of the age distribution of the stock and of the age distribution of the catch may both be quite different from the simple constant mortality form (see Jones, 1964). Sometimes, e.g. when decreased vulnerability is balanced by decreased mortality, the age distribution of the catches may be very similar to that obtained with constant mortality.

Total mortality can also be estimated from the "virtual population." The virtual population of a certain year-class on say its eighth birthday is the total number of fish of that year-class caught after their eighth birthday.

The mortality during the ninth year of life is then obtained as the logarithm of the ratio of the virtual populations at nine and at eight years old. The method is probably most useful for long-lived fish, of which fishing takes a major share, but for which "availability" varies and is difficult to measure (see Fry, 1957; Bishop, 1959; Garrod, 1967).

When the age composition is not known, estimates, and sometimes quite good estimates, of total mortality can be obtained from length data. The relative number of fish in two different size groups will depend on (*a*) the time taken to grow from one size to the other, (*b*) the mortality rate during that period, and (*c*) the time taken to grow through each size group, i.e. the proportion each size group is of a complete year-class. These factors have one particularly simple case if there is a range of sizes over which the growth is linear, or approximately so. Then if the numbers in each size group are plotted on a logarithmic scale, as for a catch-curve, the plot should yield a straight line, whose slope is proportional to the total mortality coefficient. Further,

if the growth rate is known, the absolute value of the mortality can be determined. The curve of growth in weight is generally more closely linear over a wider range of important sizes than is growth in length. Therefore a plot of numbers in each weight group against weight may provide a fair estimate of mortality. Mathematically if the growth curve over some range of age can be represented by the straight line $l_t = a + bt$ and the slope of the plot of numbers against length is Z', i.e. $\log N_l = \log N'_o - Z'l$, then $Z = bZ'$, or if the growth in weight is linear so that $W_t = C + gt$, $\log N_W = \log N''_o - Z''W$, then $Z = gZ''$.

The total mortality can also be measured in a steady state by the average age or length in the exploited population, which will, if the fishery is not selective, be the same as that in the catch. If the ages and lengths of entry into the exploited phase, and the averages in the catch, are t_c, l_c, $\bar{t}$, $\bar{l}$ respectively, the following expressions for Z can be readily derived (*cf* Beverton and Holt, 1956).

$$Z = \frac{1}{\bar{t} - t_c}; \quad Z = \frac{K(L_\infty - \bar{l})}{\bar{l} - l_c}$$

where K, L_∞ are the constants in the von Bertalanffy equation.

5.3 Fishing mortality

There are numerous methods for estimating the fishing mortality, none of which is entirely satisfactory, and in practice it is advisable to obtain estimates from as many independent methods as possible. The main methods are outlined here, dealing first with the more direct ones.

(*a*) *Direct census.* If the total stock is known, the fishing mortality can be calculated at once from the catch. The total numbers may be obtained by a complete or sample count, e.g. salmon passing upstream, or whales seen in a known area; usually, the only practicable method for marine fishes is the census of adult females by counting (by a suitable plankton survey) the number of eggs produced. The total numbers are then estimated from the proportion of adult females in the catch and their fecundity. An advantage is that it is rather easier than with most other methods to attach statistical confidence limits to the estimates, though these may be wide (see English, 1964).

(*b*) *Swept area.* From the definition of the instantaneous mortality coefficient it follows that the fishing mortality generated by a single operation, which may be considered as taking an infinitesimally small part of the whole stock, is equal to the fraction of the popu-

lation which is caught. If the stock is evenly distributed and the gear effectively catches all the fish within a certain area, a, and the total area inhabited by the stock $= A$, then the fishing mortality is equal to $\frac{a}{A}$. The mortality generated during a period of duration Δt by the whole fishery, $F\Delta t$, is then $\frac{a'}{A}$, where a' is the sum of the areas covered by all the vessels of the whole fleet. This method is, of course, confined to gear for which the area covered can be readily estimated, e.g. for a trawl haul the area covered would appear to be the distance between the doors times the distance covered. There are two important sources of error, acting in opposite directions. First, since some of the fish in the area covered by the gear may escape, the method may over-estimate the mortality. Secondly, as mentioned in the section on effort, the density of fish in the fished area will be greater than the average density, leading to an underestimate of the fishing mortality. The method therefore cannot give an exact estimate of fishing mortality, but may sometimes be useful to give an indication of its order of magnitude. In particular, it is often useful in showing whether fishing is likely to be having a significant effect. The method may also be used where the area covered by fish can be determined from an echo survey. (For uses of echo sounders, etc. in measuring abundance, and hence fishing mortality, see International Council for the Exploration of the Sea, 1964b, Symposium on the Measurement of the Abundance of Fish Stocks, especially papers by Cushing and Federov, and FAO, *Report of ACMRR Working Party on Direct and Speedier Estimation of Fish Abundance*, 1967.)

(*c*) *Marking*. Marking experiments are, of course, one of the best known methods of estimating the fishing mortality. If the population of marked fish is in all ways the same as the total stock, the fishing and total mortalities are readily determined from the number of marked fish returned. The methods are discussed in the next section.

(*d*) *Changes in total mortality*. If the amount of fishing changes, thus changing the fishing mortality, this will result in a change in total mortality. Thus if observed changes in the latter can be related quantitatively to known changes in fishing effort, the value of the fishing mortality coefficient at any given level of effort can be deduced. Mathematically, we have for a period of duration, T,

$$ZT = (F + M)\,T = qf + M\,,$$

where f is the total effort during the period.

If $T = 1$, then, using the data of effort during one year

$$Z = F + M = qf + M \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (5.6)$$

or, in terms of the fishing intensity $\left(\frac{f}{AT}\right)$,

$$Z = \frac{qf}{AT} + M.$$

If a series of pairs of values of f (fishing effort) and Z (total mortality coefficient) are known, equation (5.6) gives a linear relation between them. For two such pairs this gives two simultaneous equations which can be solved for q and M. For more than two pairs the plot of Z against f should yield a straight line, slope q, and intercept on the y-axis M (see Figure 5.2).

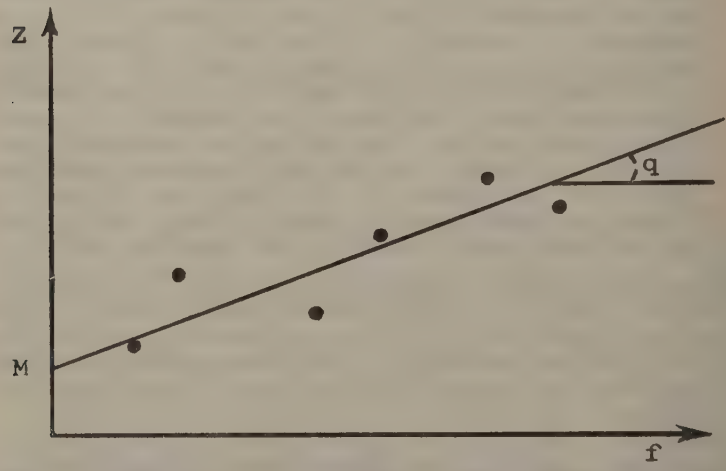

FIGURE 5.2. – Estimation of F and M. Plot of mortality coefficient against fishing effort.

The solution for q and M can be obtained by the normal regression techniques of statistics, for equation (5.6) is in the standard form for a linear regression

$$y = a + bx$$

where y = total mortality coefficient: x = fishing effort.

Denoting by $\bar{x}, \bar{y}$ the mean values of x and y, the least squares estimates for M and q are

$$q = b = \frac{\Sigma (x - \bar{x})(y - \bar{y})}{\Sigma (x - \bar{x})^2} \quad \ldots\ldots\ldots\ldots\ldots\ldots (5.7)$$

$$M = a = \bar{y} - b\bar{x} \quad \ldots\ldots\ldots\ldots\ldots\ldots (5.8)$$

The correlation coefficient, the significance level of the regression, and the confidence limits of M and q can be calculated by the standard techniques.

If the mortalities used in the regression have been estimated from indices of abundance at known instants in time, i.e. from equation (5.1), the results of the regression can be used at once. Thus the mortality between 1 January 1961 and 1 January 1962 can be related to the total fishing effort in 1961. More usually the indices of abundance will be known only as averages over a period — e.g. as the mean catches per unit effort in 1961 and in 1962. As equation (5.2) shows, the mortality estimated from the ratio of the two indices of abundance (i.e. log $\bar{N}_1/\bar{N}_0$) will be related to the mortalities (and hence fishing effort) in both periods. The mortality should therefore be related to the average of the total fishing effort in the two periods. Thus, for example, graphically we would plot the log ratio of the mean numbers in 1961 and 1962 against the average effort in 1961 and 1962. It can be shown that this method does in fact make the most efficient use of the data (Paloheimo, 1961).

This method, though most obviously used for effort varying with time, i.e. from year to year, can also be applied when the fishing effort varies with age, supposing that a selective gear is in commercial use, but that true density indices of each age group can be obtained, e.g. by special research vessel sampling.

When the estimates of mortality between successive pairs of years are highly variable, because of sampling errors or other causes (e.g. changes in "availability") rather than real changes in mortality, an average mortality coefficient over several years can be obtained by following the fortunes of a single year-class throughout its life in the exploited phase. If its density index is plotted on a logarithmic scale this should yield a straight line, slope equal to the mortality coefficient, and this last can be plotted against the average fishing effort in the corresponding period. Though this method gains in reducing the scatter, this is at the cost of losing information on the effect of year-to-year changes, though not of long-term trends, in fishing effort. Also, since the data for adjacent year classes come to a large extent from the same years, the points are not fully independent, and the exact tests of significance and confidence levels, outlined above, also cannot be applied.

5.4 Natural mortality and growth characters

An idea of the value of the natural mortality rate can be gauged from the growth pattern of the species concerned. A fish which approaches its ultimate length quickly — i.e. has a high value of K — is likely to have a high natural mortality, whereas a fish that grows slowly (a low K) is likely also to have a low M. The relation between M and K appears to differ from one group of fish to another — thus for clupeoids M is generally between one and two times K; for gadiforms M is generally between two and three times K. Like the swept area method for estimating fishing mortality this is not a precise method, but is often most useful in the early stages of studying a fishery in judging whether natural (or fishing) mortality is likely to be the dominant element in the total mortality (Beverton and Holt, 1959).

5.5 Special graphical methods

Graphical methods can also be used to estimate mortality rates from some other special situations where algebraic methods would be difficult. Regier (1962) has described some such situations where census data giving the stock in absolute numbers at different times are available and also statistics of total catch, either during a very short season (perhaps only a few days, so that fishing mortality is extremely high) or during a season covering only a part of the period between the two census dates.

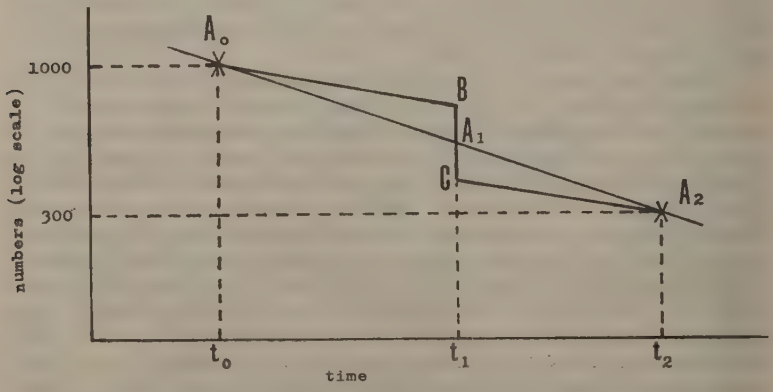

FIGURE 5.3. – Graphical method for determining mortality rate.

Consider first a very short fishing season, during which 300 fish are caught in, say, two days. At some time, t_0, before the season say 1 000 fish were present, and at some time t_2 after the season say 300 fish were present. Using semilogarithmic paper, as in Figure 5.3, the population sizes at the two census dates are given by points A_0, A_2. If the mortality rates had been constant the population at the time of the fishing season, t_1, would have been A_1. In fact the real changes in the population would be described by the line A_0BCA_2 in the figure where BC represents the catch of 300 fish, and the two parallel lines A_0B, CA_2 the decrease due to natural mortality. As the two triangles A_0BA_1, A_1CA_2 are similar the ratio of the lengths $BA_1 : A_1C$ (as measured by a ruler on the semilogarithmic paper) will be equal to the ratio of the periods $(t_1 - t_0) : (t_2 - t_1)$. As a first approximation take some position of C and the position B at a value of $C + 300$. Measure with a ruler the distance BC (this distance will vary with the value of C). Then the distance CA_1 as measured with a ruler should be equal to $\frac{BC\,(t_2 - t_1)}{(t_2 - t_0)}$. If it is greater than this the first approximation of C is too low; the correct value of C can thus quickly be found. The natural mortality is then readily determined from the line A_0B (or CA_2) — as usual this is most easily done by noting where it crosses the population size of 1, or 100 etc., and reading off the population size exactly one year later.

More generally, fishing takes place over a period — the open season — during which the fishing mortality can be taken as constant. Censuses are made at two times outside the fishing season, so that the time between the two censuses includes two periods before and after the open season during which only natural mortality is occurring. As a first approximation the known catch, C, may be assumed all to be taken at the midpoint of the season and, using the method described above, a first estimate of natural mortality, M_1, can be obtained. Using this value of M the deaths outside the fishing season can be calculated and hence, by subtraction, the total deaths N during the season, and the total mortality ZT (where T = duration of season) estimated.

Then F may be estimated from

$$FT = ZT \times \frac{C}{N}$$

Using this value in the equation $MT' + FT = \log \frac{N_1}{N_2}$, where N_1, N_2 are the numbers at the time of the two censuses, and T' the time between censuses, a second estimate, M_2, of natural mortality can be obtained. A third estimate of M is $M_3 = \frac{1}{2}(M_1 + M_2)$, which can be used in the same way to obtain improved estimates of F and M. (The procedure of obtaining a succession of better and better estimates is called iteration.)

5.6 Exercises

1. (*a*) A certain mortality causes 25 percent of the population to die each year; what percentage of the initial population is left after 2 years; 6 months; 3 years? What is the corresponding instantaneous mortality coefficient? (N.B. find the coefficient first.) Repeat for mortalities causing 10 percent, 90 percent, 50 percent mortalities per year.

   (*b*) Two causes of mortality, acting independently, cause mortality coefficients of 0.2 and 0.3; what is the resulting total mortality coefficient? Repeat with coefficients of 0.7 and 0.1; 1.0 and 0.3.

   (*c*) Two causes of mortality act independently on a population; alone they would cause respectively 20 percent and 30 percent of the population to die within a year. Do 50 percent of the population die within a year? If not, what is the percentage that does die (N.B. convert to instantaneous mortality coefficients)? Repeat for pairs of mortalities causing 70 percent and 30 percent; 80 percent and 70 percent mortalities.

   (*d*) Plot y against x, on semilogarithmic paper, and $\log_{10} y$ and $\log_e y$ against x on ordinary graph paper, for each set of y.

x	0	1	2	3	4	5	6
y_1	0.79	0.63	0.50	0.40	0.32	0.25	0.20
y_2	0.71	0.35	0.18	0.089	0.045	0.022	0.011

Do the points satisfy the equation

$$\log y = ax + b$$

or

$$y = c\, e^{dx}\ ?$$

If so, what are the values of a, b, c, d? (Estimate these from the slope and intercept of the straight-line relation). If the y's are indices of the density of a certain year-class of fish at yearly intervals, do the data fit constant mortality coefficients? If so, what are the fractions surviving each year, and what are the instantaneous mortality coefficients?

2. A research vessel in five one-hour trawl hauls caught the following numbers of fish at each age

I , 30 ; II , 450 ; III , 120 ; IV , 70 ; V , 25 ; VI + , 15

A year later, the catches in twelve one-hour hauls were

I , 60 ; II , 960 ; III , 480 ; IV , 120 ; V , 72 ; VI + , 42

Assuming for the purposes of this example that, with the mesh size in use, the catch per hour gives a valid index of density for two-year-old fish and older, estimate the total mortality coefficient during the year. If the only data available were those for the first of these years, give an estimate of the average total mortality during the previous few years. (In practice 5 or 12 hauls would generally be quite insufficient to provide a valid index of density.)

3. A group of fish is subject in two successive years to total mortality coefficients of 0.85 and 0.80. If the number present at the beginning of the first year is 1 000 what is the average number present in each of the two years? What is the total mortality coefficient estimated from these two averages?

4. A plankton survey showed that 2×10^{11} eggs were laid during a spawning season. Fecundity studies showed that the average mature female laid 10^5 eggs. Market studies showed that 3 000 000 fish were landed during the year following, and of these 40 percent were adult females (i.e. had spawned at least once). What percentage of the spawning females was caught during the year? If the total mortality coefficient was 1.2, what were the fishing and natural mortality coefficients?

5. The average number of plaice landed at Lowestoft per 100 hours' fishing in two periods were

Years \ Age	2	3	4	5	6	7	8	9	10
1929–38	125	1 355	2 352	1 761	786	339	159	70	28
1950–58	98	959	1 919	1 670	951	548	316	180	105

Calculate the average total mortality coefficients in the two periods. If the average total fishing efforts on plaice in the North sea during the two periods were, in terms of millions of hours fishing by United Kingdom steam trawlers, 5.0 in 1929-38, and 3.1 in 1950-58,

estimate from equation (5.6) the natural mortality, and the fishing mortality in the two periods.

6. The table below gives the age composition of cod in terms of numbers landed per 100 ton-hours fishing by United Kingdom trawlers, in the Barents sea, and the total fishing effort in each year.

Year \ Age	3	4	5	6	7	8	9	10	11	12+	Effort
1932	0.02	0.38	1.49	3.16	3.81	2.16	1.55	2.20	1.48	2.80	174
1933	—	0.37	2.12	3.37	4.62	3.37	1.60	1.37	0.64	2.18	184
1934	—	0.43	3.18	6.18	5.47	8.69	2.59	0.75	0.56	1.98	164
1935	0.03	0.56	7.85	13.97	10.04	5.82	2.82	0.88	0.29	1.22	184
1936	0.1	0.58	1.75	8.61	7.96	9.28	3.50	0.93	0.19	1.13	252
1937	0.02	1.89	2.91	7.66	17.05	8.65	2.53	0.38	0.26	0.33	321
1938	0.4	1.87	7.09	5.73	9.46	9.54	4.30	1.24	0.48	0.13	253
1946	7.3	11.52	11.39	18.91	13.77	11.77	14.29	17.65	5.26	3.13	66
1947	2.1	18.25	28.42	28.42	22.57	5.99	7.10	10.45	11.01	4.74	103
1948	0.9	1.89	15.59	33.19	26.77	11.31	7.17	2.01	3.65	2.76	156
1949	4.4	12.92	18.38	34.83	20.08	9.08	6.58	2.94	1.59	2.50	171
1950	—	0.49	1.15	5.49	12.89	9.32	4.28	1.76	1.01	0.37	248
1951	0.04	1.41	8.61	13.58	11.52	6.62	4.11	1.76	1.96	0.02	313
1952	0.15	4.65	11.84	16.26	13.14	4.09	2.11	1.52	0.91	0.93	412
1953	0.02	2.02	13.77	16.41	7.20	5.49	1.62	0.70	0.15	0.25	396
1954	0.07	5.33	19.03	21.76	20.25	3.99	1.62	0.48	0.67	0.13	425
1955	—	0.73	10.83	26.82	15.70	5.44	1.93	1.30	0.57	0.19	551
1956	0.02	0.50	6.29	22.76	13.51	5.59	1.20	0.61	0.24	0.08	630
1957	0.08	1.98	3.40	9.81	9.70	6.55	1.29	0.58	0.38	0.10	457
1958	0.6	4.4	9.98	8.31	5.81	5.53	1.56	0.91	0.42	0.20	414

Tabulate the total mortality coefficient for each pair of years for each age. Examine the data and decide from what age the fish are fully represented in the catches. What evidence is there that the age at full recruitment is different in the pre- and post-war periods? Hence obtain a single estimate for the mortality between successive pairs of years (take the ratio 7 and older; 8 and older). By relating this mortality graphically and by calculation of the regression line to the average fishing effort in the two years, estimate the natural mortality and the fishing mortality in 1958. What are the confidence limits to the natural mortality? (Note that the estimate of M obtained will, as usual, include any net migration from the fished area.)

SECTION 6. TAGGING

6.1 Data for mortality rates and population size

Tagging of fish can be used in studying growth, and movements and migration. This section, however, is concerned only with the use of tagging data to determine the mortality rates of the population, and the size of the population. (Growth is referred to in section 3.) The simplest assumption is that the tagged fish are subject to constant fishing and natural mortality rates which are the same as in the natural untagged population, and these can be estimated separately, because, unlike the natural population, the initial number in the tagged population is known precisely.

That is, if N_o fish are tagged at a certain moment, the number N_t alive after time t is given by

$$N_t = N_o e^{-(F+M)t} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (6.1)$$

The rate at which these are caught is equal to the fishing mortality coefficient times the number alive and is therefore given by

$$\frac{dn}{dt} = FN_t = FN_o e^{-(F+M)t}$$

where n = number of tagged fish recaptured.

The total number of returns from $t = o$, the time of tagging up to time T is therefore obtained by integrating, i.e.

$$n_T = \int_o^T \frac{dn}{dt}\, dt = \int_o^T FN_o e^{-(F+M)T}\, dt$$

$$= \frac{FN_o}{F+M}\left\{1 - e^{-(F+M)T}\right\}$$

If the returns are grouped in time intervals of length T, the number n_r caught during the rth interval between times rT, $(r + 1)\,T$ is therefore

$$n_r = N_o e^{-(F+M)rT} \frac{F}{F+M} \left\{1 - e^{-(F+M)T}\right\} \quad \ldots\ldots\ldots (6.2)$$

(Note: The first interval after tagging is $r = o$.)

The number caught in successive intervals can therefore be used, knowing N_o, to give estimates of F and M. In particular,

$$\log n_r = -(F + M)\, rT + \log \left\{ \frac{FN_o}{F+M} (1 - e^{-(F+M)T}) \right\} \quad \ldots (6.3)$$

so that if log n_r is plotted against r, the result is a straight line, slope $-(F + M)\,T$. (An alternative and rather more convenient form of this equation is given in equation [6.9].) Using this value of $(F + M)$, F can be estimated from the numbers returned in any interval, using equation (6.2), or from the intercept of the y-axis, which from equation (6.3) is

$$\log \frac{FN_o}{F+M} \left\{1 - e^{-(F+M)T}\right\}$$

Alternatively, the total number of returns up to time t is

$$\frac{FN_o}{F+M} \left\{1 - e^{-(F+M)t}\right\}$$

from which, substituting for $F + M$, a direct estimate of F can be obtained. When t is very large this reduces to $\frac{FN_o}{F+M}$.

Unfortunately the assumptions made on this simple example are not often fulfilled. The types of errors which may arise can be placed in definite groups, according to their effect on the various estimates.

(*a*) Errors which affect the estimate of the rate of fishing (F), but not the estimate of total mortality (Ricker's type *A*, Beverton and Holt's type 1):

(i) death of fish immediately after tagging;

(ii) incomplete reporting of tags recaptured by fishermen (provided the proportion not reported stays constant; a variable reporting rate would also affect the estimate of total mortality).

(*b*) Errors which affect the estimate of the total mortality, but not that of fishing (Ricker's type *B*, Beverton and Holt's type 2):

(i) loss of tags from fish which occurs at a steady instantaneous rate throughout the experiment;

(ii) additional mortality of tagged fish, also occurring throughout the experiment;

(iii) emigration of tagged fish.

(*c*) Errors affecting estimates of both fishing and total mortality:

(i) tagged and untagged fish not equally vulnerable to fishing, e.g. the additional likelihood of fish tagged with Petersen disks to be retained by a net;

(ii) tagged fish not uniformly mixed with the untagged population.

Type (*a*) errors will lead to an underestimate of the true fishing mortality, which in itself may often be useful. They can often be detected and possibly measured by suitable observations. Thus in suitable conditions tagged fish can be kept in tanks or cages and their mortality for the period after tagging can be directly observed. Less directly the percentage returns of fish which when tagged were in different conditions — lively or not so lively, damaged or apparently undamaged, etc., or captured by different methods — can be compared. If there is any mortality due to the shock of capture and tagging then it will presumably be lower for lively fish, and higher for bruised or damaged fish (loss of scales often appears to be particularly critical). Absence of such difference can be taken as an indication, though not proof, of little or no such mortality.

Nonreporting of tags can often be detected by comparing the number of tags returned per unit quantity of fish caught by various groups of vessels fishing in the tagging area — individual boats, different countries, etc. It may be directly measured by feeding known numbers of tagged fish into the catches; this is general practice with mechanical methods of recovery (e.g. magnets at fish meal factories), but can, particularly with the co-operation of a few fishermen, be used for normal external tags returned by fishermen or shore workers.

Type (*b*) losses can be considered as an additional cause of mortality, i.e. loss of individuals from the population of tagged fish, so that equation (6.1) should be written as

$$N_t = N_0 e^{-(F+X)t} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (6.4)$$

where X includes all causes of reduction of tagged fish other than fishing — loss of tags and emigration as well as natural mortality. Equation (6.4) and the corresponding form of equation (6.2)

$$n_\tau = N_0 e^{-(F+X)T_\tau} \frac{F}{F+X} \left\{ 1 - e^{-(F+X)T} \right\} \quad \ldots\ldots\ldots \quad (6.5)$$

will be the usual form for analysis of tagging data, so that in fact only the fishing mortality of the natural population will be estimated from tagging. Natural mortality will be given by subtraction from the total mortality, Z, estimated from age composition, etc.

Some quantitative estimate of type (*b*) losses can sometimes be obtained, for instance losses of tags (but not mortality of tagged fish) can be estimated by attaching two tags to each fish and noting the proportion of fish returned with both tags, and with only one tag, and the change in this proportion with time.

Differential vulnerability to fishing of tagged fish can usually be eliminated by suitable design of tags. Fish carrying button-type tags are likely to be particularly vulnerable to certain types of gear — e.g. set nets — and if possible such tags should not be employed where this type of gear is used, but if they have to be used, or in order to interpret past data, the extent of the extra fishing mortality can be gauged by comparing the rate of return of fish with different types of tags.

6.2 Varying distribution in space

A distribution of tagged fish different from that of untagged fish is likely to present one of the major problems. If mixing is relatively quick, returns during some initial period, O to t', during which the tagged fish are mixing with the untagged population, may be omitted in the computations. The analysis is then carried on from time t', with a reduced initial number of tags, using equation (6.1) in the form

$$N_t = N_o' e^{-(F+X)(t-t')} \quad \ldots\ldots\ldots\ldots\ldots \quad (6.6)$$

N_o' is estimated from the number tagged, subtracting the number returned in the initial period of mixing, and the estimated number lost through other causes, X. This last estimate will have to come from an analysis of the later data. However, in many situations nearly all returns will be made before the tagged and untagged populations are even approximately mixed.

This mixing may be effectively speeded up by a suitable pattern of tagging. The aim is to have the ratio of tagged to untagged fish the same throughout the population. This might for instance be achieved by making an evenly spaced grid of trawl stations covering the whole area, and tagging all, or a constant proportion of, the fish caught at each station. This is possible in a small area but not easy to do in, say, the North sea.

In a large area such as the North sea it may not be possible to ensure effective mixing of tagged and untagged fish, or at least by the time the mixing has occurred most of the returns have taken place, and to ignore returns occurring before mixing was effectively complete would

mean discarding most of the available data. However, if good information is available on the geographical distribution of the fishing effort, and on the positions of the capture of the returned tags, useful estimates of the fishing mortality on the untagged population can be made. The logical steps are:

(*a*) Estimate the fishing mortality, F, on the tagged population.

(*b*) From the distribution of fishing effort and of the tagged fish estimate the fishing intensity, f, on the tagged population.

(*c*) Hence estimate q, in the relation $F = qf$.

(*d*) Estimate the fishing intensity on the whole population.

(*e*) Hence, assuming that q for tagged and untagged fish is the same, estimate the fishing mortality on the whole population.

It should be noted that, especially in the first steps, it is not necessary to consider fishing by all vessels, or in all areas, provided the same section of the total is used in computing fishing mortality (from returns of tags) and fishing intensity (from data on fishing effort). For instance, in the North sea some of the most extensive detailed data on fishing effort is of fishing by United Kingdom deep-sea trawlers; it therefore may be convenient to compute the fishing mortality and intensity only from the data of United Kingdom trawlers, and ignore returns of tags, and fishing activity by United Kingdom seiners and inshore vessels, and by vessels of other countries.

Consider a small area around the position of tagging in which mixing of tagged and untagged fish takes place quickly. For a certain time interval, i, let

$\bar{N}_i$ = mean number of tagged fish present

f_i = fishing intensity (effort per unit area per unit time)

n_i = number of tagged fish returned.

Then

$$\frac{n_i}{f_i} = q\bar{N}_i \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (6.7)$$

If then $\frac{n_i}{f_i}$, the tags returned per unit fishing intensity, is plotted against time, and a curve fitted to the points, the intercept of this curve on the y-axis will be qN_o, where N_o is the number released. Hence q can be estimated and the fishing mortality on the population as a whole will be given by

$$F = q\bar{f}$$

where $\overset{\circ}{f}$ is the effective overall fishing intensity on the population, as calculated from detailed effort statistics.

While the following assumptions may not be completely justified, to a first approximation the fishing intensity within the small area chosen around the release point may be taken as constant, and the movement out of this area defined by a constant exponential coefficient, D, and therefore the number of tagged fish in the area after time t, N_t, will be given by

$$N_t = N_o\, e^{-(F+X+D)t}$$

where F is the fishing mortality occurring in the area around the release point, and not necessarily that in the population as a whole. If the ith interval is of duration T, and extends from time $(i - \frac{1}{2})\,T$ to $(i + \frac{1}{2})\,T$

$$\bar{N}_i = N_o\, e^{-(F+X+D)\left(i-\frac{1}{2}\right)T}\,[1 - e^{-(F+X+D)T}]\,\frac{1}{(F+X+D)\,T}$$

or

$$\bar{N}_i = N_o\, e^{-(F+X+D)iT}\left[\frac{e^{\frac{1}{2}(F+X+D)T} - e^{-\frac{1}{2}(F+X+D)T}}{(F+X+D)\,T}\right] \quad \ldots\ldots \quad (6.8)$$

Thus, so long as $(F + X + D)\,T$ is small, i.e. the numbers do not change very greatly during one interval, to a close approximation the term in the brackets will be equal to unity

$$\bar{N}_i = N_o\, e^{-(F+X+D)iT} \quad \ldots\ldots\ldots\ldots\ldots \quad (6.8')$$

and the plot of $\frac{n_i}{f_i}$ against time should be a straight line if plotted on a logarithmic scale. It may be noted that equation (6.8), and particularly its approximate form (6.8′) suggests a good alternative to equation (6.3) in the form

$$\log n_r = -(F+M)(r+\tfrac{1}{2})\,T + \log FN_oT$$

$$+ \log\left[\frac{e^{+\frac{1}{2}(F+M)T} - e^{-\frac{1}{2}(F+M)T}}{(F+M)\,T}\right] \quad (6.9)$$

where again the last term may be neglected if the change in numbers during the interval is small, i.e. if the logarithm of numbers recaptured during each interval is plotted against the midpoint of the interval, then the plot should be a straight line, slope $-(F + M)\,T$, and intercept on the y-axis log $FN_0\,T$.

Equation (6.7) can be extended to cover data from more than one small area around the release point. Denoting values for particular areas by prefixes

$$\bar{N}_i = \Sigma_j\, \bar{N}_i$$

when $\bar{N}_i$ = total of tagged fish in the areas being analysed

$_j\bar{N}_i$ = number of tagged fish in the jth area.

$$q_j\, \bar{N}_i = \frac{{}_jn_i}{{}_jf_i}$$

and therefore

$$\Sigma\, \frac{{}_jn_i}{{}_jf_i} = q\, \Sigma\, {}_j\bar{N}_i = q\bar{N}_i \quad \ldots\ldots\ldots\ldots\ldots \quad (6.10)$$

so that the analysis can be carried out as before, using the sum of the tags returned per unit fishing intensity in each small area. The analysis can be carried out only when sufficient effort data are available; if tags are returned from a mixed fleet, some of which provide adequate effort data and some of which do not, then in all the analysis only data from the fleet or fleets providing complete data both of effort and tags returned should be used. Tagged fish caught by the other fleet are considered as other losses. Data from the other fleet are brought into the considerations only at the end, when computing the fishing mortality on the population as a whole.

6.3 Exercises

1. Graham (1938) tagged 1 000 cod in the North sea, and the following numbers were returned, grouped in three-monthly intervals.

Months	0–2	3–5	6–8	9–11
Numbers	139	91	52	40

By plotting the logarithm of the numbers returned against time, estimate the total and fishing mortality coefficients. (Compare the results of using equation [6.3] and the approximate form of equation [6.9].)

2. Whiting tagged and released in the Irish sea were graded according to their liveliness and the damage to their scales, and the numbers released and subsequently recaptured were as follows (data from Beverton and Bedford, 1963).

Condition	Scales	Number tagged	Number returned
Lively	Good	60	18
Lively	Moderate	98	21
Lively	Poor	49	6
Sluggish	Good	254	60
Sluggish	Moderate	765	159
Sluggish	Poor	509	43

What evidence is there of mortality at tagging? Assuming all the best quality fish survived, what proportion of each other category died, and what was the effective number released?

3. From cod tagged in the Gulf of Saint Lawrence in 1955, the following numbers were returned by different countries in 1956 (from Dickie, 1963).

Country	Number of tags	Total cod landings
		tons
Canada	392	62 400
France	32	28 000
Portugal	29	5 800
Spain	15	8 100

Calculate the number of tags returned per 1 000 tons of fish landed by each country. What evidence is there of incomplete returns? If all tags recaptured by Canadian fishermen are returned, estimate the number actually recaptured by other countries.

4. Three groups of herring tagged with internal tags were released in the North sea in the summer of 1957. Detailed data of Danish fishing intensity in the areas around the release points were available, in terms of hours' fishing per statistical square (15 × 15 miles).

The number of tags returned, and the fishing intensity around each tagging position in the weeks following tagging, were as follows (data adapted from International Council for the Exploration of the Sea, 1961).

Week after tagging	Liberation number					
	1		2		3	
	Tags	*Intensity*	*Tags*	*Intensity*	*Tags*	*Intensity*
1	21	80	80	420	3	10
2	35	64	12	60	3	5
3	30	53	10	50	8	15
4	8	26	2	10	2	10
5	10	56	1	10	—	—
Number tagged	3 000		1 500		3 000	

Plot the tags returned per hours fishing per square for each liberation. Hence, if the efficiency of the recovery technique is such that 90 percent of the tags caught are returned, what is the value of q, in terms of an intensity of 100 hour's fishing per square per week?

SECTION 7. RECRUITMENT AND SELECTION

Not all sizes or ages of fish undergo the same fishing mortality: small fishes may escape through the meshes of a net, or not be in the main fished area. It is useful to distinguish the part due purely to behaviour (in the widest sense) of the fish themselves — recruitment — and that due to the properties of the gear selection.

7.1 Trawl selection

Selection is simplest in the bag-type of gear — trawls, seines, etc. For these gears it is usual to assume that the size composition of the fish entering the mouth of the net is the same as that in the immediate vicinity of the gear. The selectivity of such gears therefore becomes a question of escape, through the meshes, of fish which have entered the net. For many species there is evidence to show that most of this escape occurs through the cod-end. Selectivity can therefore be determined directly if the numbers of each size of fish entering the net can be estimated, either by attaching a small-meshed cover over the cod-end or other parts, or from the size-composition of the catches of nets of much smaller meshes fished at the same time and place. Whichever method is used, the results can be expressed as the proportion of fish at each length entering the net which are retained in the cod-end. When these proportions are plotted against length, the selection curve of the net for the species concerned is obtained. A typical example is shown in Figure 7.1.

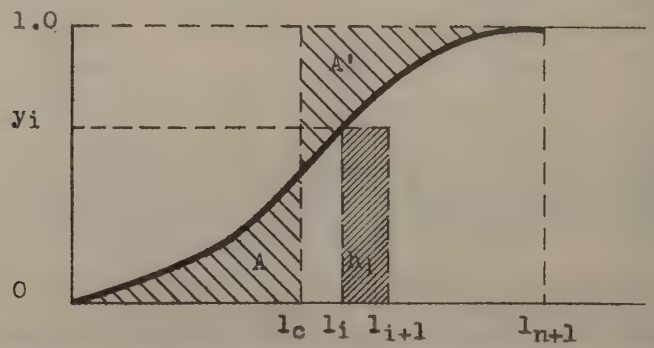

FIGURE 7.1. – Simple selection curve. Determination of mean selection length.

A selection curve may extend over a range of length of fish of perhaps 10 cm or more, which means that as young fish begin to grow into the selection range they at first suffer only a low fishing mortality. As they grow larger, their chance of escaping from the net (having entered it) gets less, until, eventually, they are too large to escape at all; only then are they exposed to the full fishing mortality rate — whatever that may be. Although it is possible to introduce this progressive change of fishing mortality coefficient over the selection range into yield assessments, it is usually sufficient to represent the selection process by a single mean selection length l_c, and assume that all fish of length less than l_c are released, and that all those greater than l_c are retained by the gear, and experience the full fishing mortality.

The important quantity is therefore

t_c = mean selection age

= mean age of entry to the catch, or mean age at first capture

In Figure 7.1 the mean selection length l_c is the length which makes the two shaded areas A and A' equal. If the selection curve is symmetrical, or nearly so, this will be the length at the midpoint of the curve, i.e. the 50 percent length, at which half the fish entering the net escape and half are retained. If the curve is not symmetrical, l_c can be calculated by equating the two areas between the selection curve and the y-axis, and between the line $l = l_c$, and the y-axis. Suppose the lengths are classified, the ith class being of size h_i and limited by the lengths l_i and l_{i+1}; the corresponding ordinate to the ith class is y_i where $i = 0, 1, 2, \ldots n$.

Then the area to the left of the selection curve is equal to the area of the rectangle of height 1 and base l_{n+1} minus the area under the selection curve. This last area can be approximated by the sum of the rectangle areas for each length-class, i.e., $\Sigma h_i . y_i$. The total area to the left of the selection curve is therefore $l_{n+1} - \Sigma h_i y_i$ which, as the total height of the curve is 1, will equal l_c. If h_i is constant and equal to 1 cm, $l_c = l_{n+1} - \Sigma y_i$.

For trawls, the mean selection length l_c is generally proportional to the mesh size, m, i.e.

$$l_c = b.m$$

where b is the selection factor

This expression enables the mean selection factor for any mesh size to be estimated from the results of experiments with a small number of different mesh sizes. The selection factor also does not vary much for fish of roughly the same shape. There is some variation in selection factor with the condition of the fish, and also with the material and construction of the meshes; light flexible materials (e.g. nylon) give higher selection factors than thicker materials (e.g. manila).

Besides the mean selection length (50 percent point) selection curves also differ in their sharpness — whether selection occurs over a small or wide range of sizes. This is usually measured by the selection range — the difference between the lengths at which 25 percent and 75 percent of the fish are retained by the gear.

7.2 Recruitment

Recruitment is the process in which young fish enter the exploited area and become liable to contact with the fishing gear. This may involve an actual movement, as in the North sea plaice, which moves, when relatively old (about three to four years), from the shallow nursery area along the coast into the main fishing grounds. Recruitment may involve only a change in habit, such as in the North sea haddock, where young and old occur in the same areas, with the very young fish being pelagic, and recruiting to the exploited phase when they take up a demersal habitat in the autumn of their first year of life. Mathematically, the important quantity is t_r = mean age at recruitment.

Recruitment is, by its nature, much less easy to express in quantitative terms than mesh selection. As the main interest is in the combined effect of recruitment and selection — i.e. the pattern of entry into the catch — the recruitment pattern is very important when it is above, or overlaps, the range of gear selection, but not when it is complete before gear selection starts. If therefore all fish have been recruited at a size below the selection range of any likely mesh size, then the precise pattern of recruitment may be ignored, and it can be taken arbitrarily as occurring at some convenient length or age below the selection range (see Figure 7.1). Where important, the general form of the recruitment curve may be determined by a proper knowledge of the biology of the species, and possibly estimated with greater accuracy by surveys, with research vessels, of the young fish both on and off the main fishing grounds. Failing this an estimate may be obtained by comparing the size composition of actual catches of commercial vessels with the known selectivity of the gear in use. Normally the recruitment will occur over a range of sizes and may be described by the same type of curve as the selection curve of Figure 7.1.

If selection and recruitment are occurring over the same range, as in Figure 7.2, then the effective selection, i.e. the proportion P_l of the full fishing mortality to which the fish of a given size in the stock are exposed will be given by the equation

$$P_l = r_l \times S_l \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (7.1)$$

where

r_l = proportion recruited, i.e. ordinate of recruitment curve,

S_l = proportion of those entering the net which are retained, i.e. the ordinate of the selection curve.

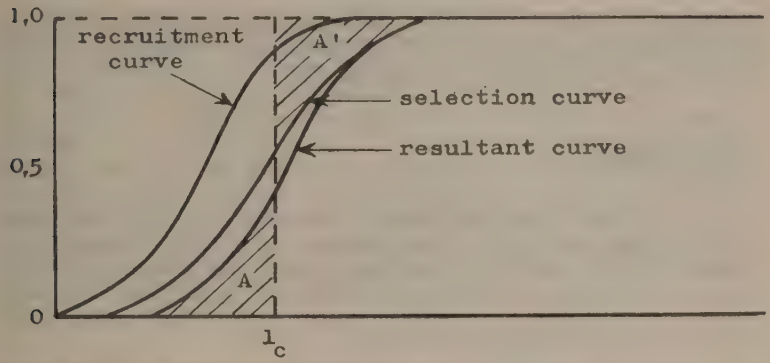

FIGURE 7.2. – Combination of a selection curve and recruitment. Recruitment over a spread of lengths.

Thus the resultant selection curve, which expresses the effective entry of fish to the catch, is obtained as the product of the recruitment and mesh selection curves, and from it the resultant mean selection length can be determined as before by equating the two areas A, A'.

Sometimes, as in cases where the recruits migrate into a fishing area, recruitment, in terms of length, can be quite sharp, approaching in the extreme case knife-edge selection at a threshold length l_r, as in Figure 7.3. Fish below length l_r suffer no fishing mortality at all, since they are not within the range of the gear. But on reaching length l_r they are at once exposed to a high fishing mortality (as drawn in Figure 7.3 more than half of the full fishing mortality). The resultant selection curve in this case therefore starts at length l_r and rises vertically to the selection curve of the gear; thereafter it is identical with the selection

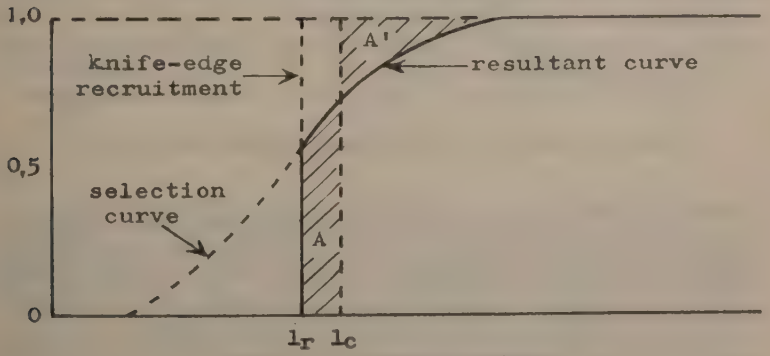

FIGURE 7.3. – Knife-edge recruitment.

curve itself. Again, however, the mean selection length l_c can be calculated from this resultant curve, in this case l_c is such that the two areas A and A' of Figure 7.3 are equal.

7.3 Size limits

If a minimum legal size limit, l_s say, is set within or above the selection range of the gear in use, the entry to the landed catch can be represented by a curve which starts at l_s, and rises vertically until the true selection curve is reached (see Figure 7.4). The mean selection length l_c is calculated in a similar way and is such as to equalize the areas A and A' of Figure 7.4.

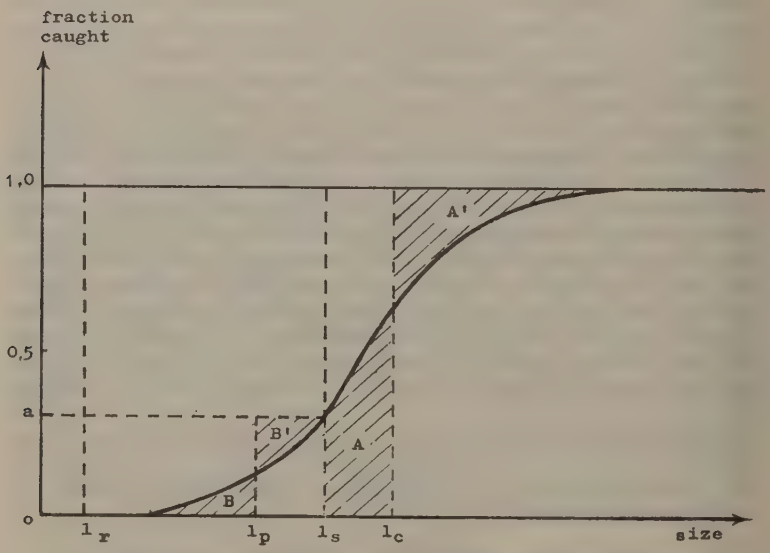

FIGURE 7.4. – Effect of size limit (l_s) on the effective selection curve.

Undersized fish will also be taken, and since they cannot be landed they must be rejected at sea. The effect of this capture and rejection on the yield from the stock depends on how many of the rejected fish survive. If all survive, the situation is the same as if the recruitment curve to the landed catch were the true selection curve.

If on the other hand, some or all undersized fish die after rejection, each year-class is subjected to a certain fishing mortality before

it reaches length l_s, as represented by the lower part of the selection curve in Figure 7.4. The resultant fishing mortality coefficient which takes account of the capture and rejection of undersized fish is obtained by calculating the mean of that part of the selection curve which is below the size limit. Calling this mean length l_p, then it is such as to equalize the areas B and B' of Figure 7.4. In other words, it is assumed that fish are not caught at all until they reach length l_p, and are then subjected to the constant fraction a of the full fishing mortality rate until they reach size l_s (a is the ordinate at length l_s, see Figure 7.4). If growth from length l_p to length l_s occupies a period $t_s - t_p$ (see below) and the fraction q of rejected fish die, then the year-class is reduced by the factor

$$e^{-qaF(t_s - t_p)} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (7.2)$$

as a result of capture and rejection of undersized fish before it enters the marketable size range. In this expression F is the full fishing coefficient to which fish are exposed when they have grown beyond the selection range of the gear.

7.4 Gill-net selection

The selectivity of gill-nets is such that the proportion of fish retained is a maximum at some optimum size, and falls off for fish bigger or smaller than this optimum. If the size distribution of the fish in the fishing area can be determined directly by using some gear which is nearly unselective, or where selectivity is known, e.g. a trawl, then the selectivity of the gill-net may be determined at once. That is, if the numbers of a given size, l, of fish caught per unit fishing time by gill-nets and the presumed nonselective gear are ${}_GC_l$, ${}_TC_l$ respectively, the fishing mortality exerted by the gill-net on fish of length l will be proportional to

$$\frac{{}_GC_l}{{}_TC_l}$$

When a nonselective gear cannot easily be used, then the selective properties are best estimated by using a range of gill-nets of several different sizes. For any particular size of fish the distribution of catches by different mesh sizes will be analogous to the distribution of catches by a particular mesh size of different sizes of fish, having a maximum at some optimum mesh size, and falling off at each side. From the data of catches by different nets (adjusted if necessary to allow

for different total fishing time by different mesh sizes) such distributions can be obtained for each size of fish. These can be combined by expressing both variables in standard terms — mesh size as the ratio of its perimeter to the girth of the given size of fish, or as a ratio of its size to the most efficient mesh size for that size of fish, and numbers of fish caught as a ratio of the numbers caught with the mesh used and with the most efficient mesh (see McCombie and Fry, 1960; Gulland and Harding, 1961).

If it is assumed that each mesh has the same optimum fishing power, i.e. causes the same fishing mortality on the size of fish for which it is most efficient, then the combined data can be used at once to give not only the relative efficiencies of different nets on a given size of fish, but for a net of a given mesh size, the relative efficiencies on different sizes of fish, i.e. its selectivity.

The selectivity may also be estimated by comparing catches of only two mesh sizes, provided some assumption is made concerning the form of the selection curve. This is often close to normal, and if it is assumed in fact to be normal, then putting

C_l = catch of fish of length l per unit fishing time

$$C_l = N_l p_m \exp\left(-\frac{(l - l_m)^2}{2 S_m^2}\right)$$

where N_l = number of fish of length l liable to capture by the gear

p_m = fishing power of net of mesh size m

l_m = length of fish for which the mesh size m is most efficient

S_m = standard deviation of the mesh selection curve

If two meshes, A and B, are fished on the same population, then, in the obvious notation

$$\frac{{}_A C_l}{{}_B C_l} = \frac{N_l p_A \exp\left(-\frac{(l - l_A)^2}{2S_A^2}\right)}{N_l p_B \exp\left(-\frac{(l - l_B)^2}{2S_B^2}\right)}$$

or, taking logarithms to base e,

$$\log {}_A C_l - \log {}_B C_l = \log \frac{p_A}{p_B} - \frac{(l - l_A)^2}{2S_A^2} + \frac{(l - l_B)^2}{2S_B^2}$$

and, if it is further assumed that the standard derivation of the selection curve is constant, i.e. $S_A = S_B = S$, this reduces to

$$\log \frac{{}_A C_l}{{}_B C_l} = \log \frac{p_A}{p_B} - \frac{l_A^2 - l_B^2}{2S^2} + \frac{l_A - l_B}{S^2} l$$

The right-hand side is linear in l, that is, can be expressed in the standard form $a + bl$, where

$$a = \log \frac{p_A}{p_B} - \frac{l_A^2 - l_B^2}{2S^2}$$

$$b = \frac{l_A - l_B}{S^2}$$

Thus if the log of ratio of the catches per unit time of nets of different size are plotted against length the result is a straight line, from which can be estimated

$$b = \frac{l_A - l_B}{S^2} = \text{slope}$$

$$a = \log \frac{p_A}{p_B} - \frac{l_A^2 - l_B^2}{2S^2} = \text{intercept}$$

From this l_A, l_B and S^2 cannot be estimated separately, and hence the selection curves determined, without some extra assumptions; however it is reasonable to assume (as in the previous section for a range of mesh sizes) that the fishing powers of the two nets are equal, and also that the optimum length is proportional to mesh size (usually in practice equivalent to a fish whose girth is slightly greater than, say 1.1 times, the perimeter of the mesh).

$$\text{i.e. } l_A = K M_A$$

$$l_B = K M_B$$

$$\text{Then slope } = b = K \frac{M_A - M_B}{S^2}$$

$$\text{intercept } = a = -K^2 \frac{M_A^2 - M_B^2}{2S^2}$$

$$\text{From which } K = \frac{-2a}{b\,(M_A + M_B)}$$

$$S^2 = -\frac{2a\,(M_A - M_B)}{b^2\,(M_A + M_B)}$$

and hence the selection curves can be determined.

Other assumptions can be made about the shape of the selection curve; in particular it might be assumed as above that the curve is normal, but that the standard deviation is proportional to the mesh size. This model often fits the observed data better than the model based on constant standard deviation (see Regier and Robson [1966] for a full review of gill-net selectivity).

When the selection curve of the gill-net has been determined, subsequent population analysis is simpler if the curve can be represented by a more simple form, analogous to the knife-edge approximation to the trawl selection. Two selection lengths are needed, l_c, the length at which the fish enter the selection range, and l_d, at which they grow out of it. That is, the fishing with a gill-net with the selection curve of Figure 7.5 has the same effect as a constant mortality between lengths l_c and l_d, where the pairs of shaded areas A and A', and B and B' are equal.

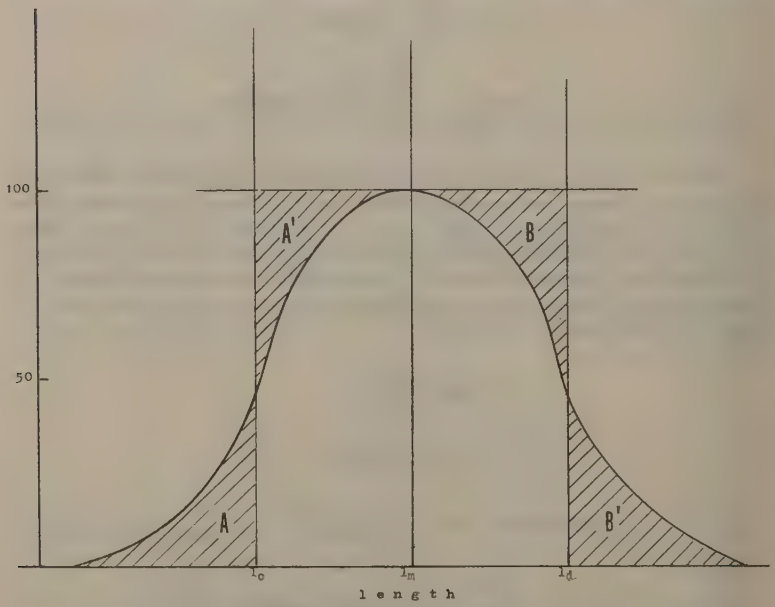

FIGURE 7.5. – Conversion of gill-net selection into a more simple form for use in population analysis, applying knife-edge approximations.

7.5 Exercises

1. (*a*) Cod-ends of 44 mm and 112 mm fished alternatively gave catches of plaice of equal fishing times as set out in Table 1.

TABLE 1. – PLAICE

Length	44-mm mesh	112-mm mesh
cm		
10	0	0
11	1	0
12	2	0
13	6	0
14	16	0
15	18	0
16	26	0
17	64	3
18	121	4
19	182	10
20	247	13
21	292	16
22	344	37
23	367	60
24	355	132
25	276	190
26	225	177
27	147	136
28	90	97
29	57	54
30	26	33
31	24	26
32	18	13
33	10	9
34	12	7
35	5	6
36	10	5
37	6	2
38	3	4
39	2	2
40	2	3
41	0	1
42	0	2
43	0	2
44	0	1
45	0	1
46	0	1
47	0	0
48	0	0

TABLE 2. – WHITING

Length	Cod-end	Cover
cm		
10	0	0
11	0	0
12	0	3
13	0	7
14	0	21
15	0	27
16	0	23
17	0	19
18	2	20
19	3	83
20	23	219
21	68	302
22	89	256
23	79	154
24	115	55
25	106	42
26	87	18
27	63	7
28	55	0
29	38	2
30	34	0
31	11	0
32	11	0
33	6	0
34	9	0
35	5	0
36	2	0
37	1	0
38	1	0
39	0	0

(*b*) A cod-end of 74 mm fitted with a small-meshed cover gave catches of whiting distributed between the cod-end and cover as in Table 2.

Draw the selection curves for plaice and whiting from these data and determine the mean selection lengths (l_c). Note that the number entering the net is for (*a*) (alternate hauls) equal to the catch in the small-meshed net, but for (*b*) is the sum of the fish retained in the cod-end, and those which went through the meshes, i.e. in the cover.

Calculate selection factors.

2. An approximate recruitment curve for the United Kingdom North sea plaice fishery is as follows:

Length (cm)	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Fraction recruited ...	0.02	0.05	0.08	0.16	0.27	0.38	0.48	0.62	0.75	0.86	0.94	0.97	0.99	1.00	1.00

Calculate the resultant selection curve with a mesh of 112 mm (using the result from Exercise 1) and hence the value of l_c.

If instead of the above recruitment curve, recruitment was found to be effectively " knife-edge " at 26 cm, what would be the value of l_c with a 112-mm mesh?

3. Convert the above estimate of l_c for plaice and whiting to age (t_c) using the von Bertalanffy equation and parameter values as follows:

Plaice: $K = 0.095$, $L_\infty = 68$ cm, $t_o = -0.8$ year

Whiting: $K = 0.32$, $L_\infty = 45.5$ cm, $t_o = -0.4$ year

4. The percentage length-distributions of cod caught by gill-nets and purse-seines at Lofoten in 1952 were as follows (data from Rollefsen, 1952)

Length (cm)	65–	70–	75–	80–	85–	90–	95–	100–	105–	110–	115–	120+
Purse-seine	2	4	8	13	20	28	35	34	25	15	8	5
Gill-nets	0	2	5	15	30	50	45	27	15	5	2	1

Assuming there is no selection by purse-seines, determine the form of the selection curve of the gill-nets. What size of fish is caught most efficiently by gill-nets?

5. Nine sizes of gill-net were used for catching salmon in the Frazer river in 1947 and 1948. The numbers of fish of sizes caught by each mesh (adjusted for different fishing times) were as follows (data adapted from Peterson, 1954)

Fork length	Mesh sizes (cm)								
	13.5	14.0	14.8	15.4	15.9	16.6	17.8	19.0	20.6
50–51	6	4							
52–53	52	11	1	1	—	—	—	—	—
54–55	102	91	16	4	4	2	—	2	2
56–57	295	232	131	61	17	13	3	1	2
58–59	309	318	362	243	95	26	4	2	1
60–61	118	173	326	342	199	100	10	8	1
62–63	79	87	191	239	202	201	39	10	6
64–65	27	48	111	143	133	185	72	16	3
66–67	14	17	44	51	52	122	74	27	3
68–69	8	6	14	23	25	59	65	51	1
70–71	7	3	8	14	15	16	34	22	2
72–73		3	1	2	5	4	6	10	1
74–75								1	

(*a*) *Graphical method.* By plotting for each size group separately the numbers caught against mesh size, estimate the numbers of each size of fish which would be caught by the most efficient mesh for that size of fish. Hence express the catch of any mesh as a percentage of the potential catch by the most efficient mesh, i.e. the selectivity of that mesh size for that size of fish.

Combine these selection curves for all meshes by expressing the mesh size as a proportion of the most effective mesh for the length group in question. Hence obtain a single combined selection curve of a gill-net on salmon.

(*b*) *Analytic method.* Calculate the logarithm of the ratio of catches of fish of a given size taken by pairs of adjacent mesh sizes. Assuming the selection curve for each mesh is normal and of constant variance, and that the mean selection length of any mesh is proportional to the mesh size, calculate the selection curve for each mesh.

B. ASSESSMENTS

SECTION 8. GENERAL PROBLEMS OF ASSESSMENT

8.1 The need for stock assessment

The previous section deals with problems of estimating the important parameters (growth, mortality, etc.) of fish populations which are of scientific interest, but not of direct interest to others concerned with fish stocks (members of the industry, administrators, etc.). It is, for instance, of no direct relevance to the practical problems of the industry that the present fishing mortality coefficient has a value of, e.g. 0.50. This section of the manual is concerned with the use of these estimates of the parameters to determine the total catch, and how the catch and the catch per unit effort (catch per boat, or catch of the individual fisherman) varies with changes in the pattern of fishing. These results are of direct practical interest — for instance, analysis showing that any increase in fishing above the present level (giving a fishing mortality of 0.50) would give no sustained increase in total catch is of vital importance for plans of possible expansion of fishing.

The problems of stock assessment occur at all stages of the development of a fishery, with the need for accuracy and precision increasing as the fishery develops. In an undeveloped fishery all that is generally required is a rough measure, say to within a factor of two or three, of the magnitude of the resource and the potential yield from it and also a measure of the decrease in catch per unit effort likely to be caused by future increases in fishing effort. These estimates may be used as bases for determining the possibilities of expansion. Later, better estimates will be required to determine when the fishery is approaching the level beyond which further expansion of fishing will give little increase in total catch, so that further expansion can be discouraged, or some form of regulation considered. Finally, in a very intense fishery, very accurate estimates may be necessary to ensure proper regulation, e.g. in setting precise catch quotas, etc.

At each stage, the scientist may be called upon to come to conclusions and give advice on the basis of data which might be considered inadequate for scientific conclusions. However, it is often essential that advice should be given, with explicit statements of its reliability where necessary, especially when a fishery is developing rapidly. For instance, in such a fishery a further expansion of say 30 percent may be actively considered. Scientific advice is required on whether the stock is fully

exploited, so that such an increase would give no increase in yield, or, at the other extreme, is very lightly exploited, so that the 30 percent increase in fishing would produce very nearly the full 30 percent increase in total catch, or somewhere between. In the absence of advice, the development might take place in the expectation that the increase in fishing will produce a proportional increase in catch, so that the action taken is effectively the same as if the scientific advice were that the resource was very lightly exploited. If, therefore, there is scientific evidence that the degree of exploitation of the stock is appreciable, this must be stated even if there is no certainty whether the increase in catch from a 30 percent increase in fishing is 5 percent, 10 percent, or 20 percent.

8.2 The concepts of sustainable yield and potential yield

In many discussions of fishery management problems, the terms " sustainable yield " and " maximum sustainable yield " are used. These are particularly, but not exclusively, used in relation to the simple population models, such as those of Schaefer (see section 10.2). These terms can often be useful in explaining the results of population analysis to administration; thus a catch equal to the sustainable yield will, on the assumptions of the simple model, leave the situation as it is. The attainment of the maximum sustainable yield is, at least apparently, a reasonable and definable objective of management, so that if the stock abundance is less than that corresponding to the maximum sustainable yield, it should be allowed to increase, i.e. less than the sustainable yield should be taken. Conversely, if the abundance is above this level, more than the sustainable yield should, on this criterion, be taken. Though a detailed discussion of the objectives of fishery management is outside the scope of this manual, it is very doubtful if the attainment of the maximum sustainable yield from any one stock of fish should be the objective of management except in exceptional circumstances. When there is a value of fishing effort which will in the long run give an average catch greater than the average catch from any other level of effort, i.e. there is a maximum in the yield/effort curve, then over some range of effort near this maximum the curve will be rather flat. Within this range a reduction of fishing effort from that giving the maximum catch will result in a decrease in catch that is much less than proportional to the reduction in effort. For economic reasons it will usually be more desirable to fish at this lower level of effort than at that giving precisely the maximum catch. Even when the objective is to harvest as much food as possible, this is most likely to be done by diverting effort to some other less heavily exploited stock.

The term sustainable yield also can be misleading, as it rather implies a degree of constancy in the situation — other than changes due

to fishing — which often do not exist. In a fluctuating fishery, e.g. one with big changes in year-class strength, it may be difficult, if not impossible, to adjust the amount caught to maintain the stock abundance at the end of the year the same as at the beginning, and when possible the catch taken would fluctuate very widely.

A more useful concept is that of the potential yield. This is the greatest average annual yield that can be taken over a period or under average environmental, non-fishery-induced, conditions, with any pattern of fishing. The actual average yield over a period will be generally less than the potential because it is impossible or undesirable (e.g. due to high costs) to employ the pattern of fishing giving precisely the potential yield. In any one year the yield may be greater or less than the potential yield, depending on such factors as year-class strength, etc.

8.3 The unit stock

Before population theory can be applied to a particular situation it is necessary to determine to what extent the fish population and the fishery based on it can be treated as a unit system. There is no simple objective definition of what constitutes a unit stock, or a unit fishery, and the definition may be made purely on practical grounds. A group of fish can be treated as a unit stock if the results of assessments and other population studies in which it is treated as a unit stock do not diverge significantly from the real situation. This means, on one hand, that happenings external to the unit stock, e.g. fishing in other areas, do not have a significant effect, and on the other hand, that there are no subgroups within the unit stock with significantly different population characteristics.

One corollary of this definition is that, as the precision of the population studies increases, the choice of unit stock may also have to change. A group of fish may have sufficiently uniform characteristics to be treated as a single stock when these characteristics are known only roughly, but may have to be treated as two or more unit stocks, perhaps with certain mixing rates, each with different characteristics, as these characteristics become measured with greater precision.

A unit stock, as used here, does not necessarily correspond to a biological, or genetic, unit. Thus, if two species in an area have the same growth pattern and mortality rates and are fished on the same grounds by the same gears, then, at least in the early stages of analysis when data are scarce, it may be permissible to treat them as a single unit stock. Conversely, male and female plaice in the North sea differ so much in growth, and in fishing and natural mortality rates, that for detailed analysis they should be treated as different stocks, i.e. yield curves, etc. should be calculated for the male and female populations

separately, and the results for the plaice population as a whole obtained by addition.

While most of this course is concerned with the simple situation of a unit stock, or unit fishery, it is worth enumerating here some of the situations which cannot be treated as a unit stock or unit fishery.

(*a*) Distinct fish stocks which intermingle for some part of the year, and are fished while mixed together. Even if the separation of fish between the stocks at the end of the mixing period is perfect, the fishing mortality of the two stocks has an element in common, and neither can be treated as a unit unless the mixed catch can be separated into the elements from each stock (? Bank and Downs herring in the North sea, ? Southern bight and German bight plaice).

(*b*) Distinct stocks, fished separately, but with a significant amount of interchange between them (e.g. Iceland and Greenland cod).

(*c*) A species inhabiting a large area with no obvious dividing features, so that any two groups of fish in adjacent areas mix freely together, but the mixing is slow enough for the fish at opposite ends of the area to be effectively independent (? many coastal species, ? North sea whiting).

A determination of what can be treated as a unit stock will be made from a wide range of information, e.g.

(*a*) Distribution of the species. This will give an upper limit to the extent of the unit stock, while the presence of more or less effective barriers, e.g. a deep water channel for a strictly demersal species, may suggest subdivisions which could behave as unit stocks.

(*b*) Spawning areas. A single compact spawning area suggests that the population is a biological unit at least so far as reproduction is concerned. Two or more distinct spawning areas suggest distinct spawning groups, though these may well mix as in types (*a*) and (*b*) above.

(*c*) Catch and effort data. Common features in records of catch and effort data for adjacent fisheries over a period may indicate that they are acting on the same stock and are parts of the same unit fishery.

(*d*) Age-composition data. Comparisons of the relative strength of year-classes in different areas may indicate the extent to which the fish in different areas are recruiting from the same source. Mortality rates, especially when combined with effort data, can be compared as in (*c*).

(*e*) Tagging. This may not always give reliable results (incomplete returns from some areas, etc.), but under favourable conditions it is a valuable technique, being especially valuable as giving a mixing rate (when mixing takes place) which can be expressed in quantitative terms.

(*f*) Morphological or physiological characteristics. Genetic differences are good evidence of groups of fish being independent stocks, but the converse is not true. Characters which may be environmentally determined (e.g. vertebral counts) are less satisfactory, since differences can exist among groups of fish which are mixing but not mixing completely.

SECTION 9. THE SIMPLE YIELD CURVE

9.1 Derivation of the equation for yield

Previous sections have been concerned with methods of collecting the basic data, and analysing them so as to obtain estimates of the basic population parameters — growth, mortality, age at recruitment, etc. This and later sections will be concerned with using these estimates to explain and understand the past history of the fishery, and to predict its future; in particular to predict the effect of changes in the pattern of fishing due to any proposed conservation or regulatory measure.

The simplest calculations are for a stock in which the various parameters are constant. For such a stock, the calculations are best made in terms of the yield of a single year-class of fish throughout its life, which will be, in the steady state, the same as the yield in one year from all year-classes present in the fishery. The whole life span can be divided into relatively short periods; for each period the number of fish alive, the number caught, the number dying of natural (nonfishery) causes, and the number surviving to the beginning of the next period can be calculated, and the yield, in weight, can be calculated as the product of the numbers caught and their average weight. This process can be done purely arithmetically, but for accuracy the periods chosen should be short, and therefore numerous, and the calculations are bound to be laborious. It is much easier to express the yield in an algebraic form, which has the great advantage of showing explicitly the influence of the various parameters on the yield.

We will define the terms as follows:

N_t = number of fish alive at age t

R = number of recruits, i.e. the number of fish alive at age t_r

R' = number of fish alive at the age t_c at which they are first retained by the gear in use

M = instantaneous natural mortality coefficient

F = instantaneous fishing mortality coefficient;

then for $t_r < t < t_c$

$$\frac{dN_t}{dt} = -MN_t$$

i.e., the instantaneous rate at which fish are dying of natural causes is equal to the product of the natural mortality coefficient times the number of fish.

$$\therefore N_t = Re^{-M(t-t_r)}, \quad \text{because} \quad N = R \text{ when } t = t_r$$

and

$$R' = Re^{-M(t_c-t_r)}$$

and for $t > t_c$, when both fishing and natural mortalities are operating

$$\frac{dN_t}{dt} = -(F + M)N_t$$

and

$$N_t = R'e^{-(F+M)(t-t_c)} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (9.1)$$

or

$$N_t = Re^{-M(t_c-t_r)-(F+M)(t-t_c)}$$

The numbers of fish caught in the time interval $(t, t + dt)$ will be $F \cdot N_t\, dt$, so that the total numbers caught, C, will be given by dividing up the total time between t_c (the age at first capture) and t_L (the maximum age attained) into short intervals, and adding the contributions from each interval.

Mathematically this is expressed by the integral (see section 2)

$$C = \int_{t_c}^{t_L} FN_t\, dt$$

$$\therefore C = \int_{t_c}^{t_L} FR'e^{-(F+M)(t-t_c)}\, dt$$

or, integrating

$$C = R' \cdot \frac{F}{F+M}\left[1 - e^{-(F+M)(t_L-t_c)}\right] \quad \ldots\ldots\ldots \quad (9.2)$$

which, if t_L is sufficiently large for $e^{-(F+M)(t_L-t_c)}$ to be neglected, reduces to

$$C = \frac{FR'}{F+M} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (9.2')$$

Thus, fishing takes a share of the total numbers reaching the age of first capture equal to the ratio of fishing mortality to total mortality.

In the same way the weight caught in the time interval t, $t + dt$, is given by

$$dY_t = FN_tW_tdt$$

where W_t is the average weight of a fish of age t.

The total weight caught will therefore be given by

$$Y = \int_{t_c}^{t_L} FN_tW_tdt \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (9.3)$$

For this to be easily integrated, the expression for the weight has to be in a suitable form; of the growth equations discussed earlier, that of von Bertalanffy is one of the most convenient. That is, we can write

$$W_t = W_\infty [1 - e^{-K(t-t_0)}]^3$$

$$= W_\infty [1 - 3e^{-K(t-t_0)} + 3e^{-2K(t-t_0)} - e^{-3K(t-t_0)}]$$

Or, writing the right hand side as a summation,

$$W_t = W_\infty \sum_{n=0}^{3} U_n e^{-nK(t-t_0)}$$

where

$$U_0 = 1, \quad U_1 = -3, \quad U_2 = 3, \quad U_3 = -1.$$

Then

$$Y = \int_{t_c}^{t_L} F.R'W_\infty e^{-(F+M)(t-t_c)} \sum_{0}^{3} U_n e^{-nK(t-t_0)}\, dt$$

or, writing $t - t_o = (t - t_c) - (t_c - t_o)$ and rearranging the terms

$$Y = FR'W_\infty \sum_{n}^{n} U_n \int_{t_c}^{t_L} e^{-(F+M+nK)(t-t_c)} e^{-nK(t_c-t_o)} dt$$

on integrating this becomes

$$Y = FR'W_\infty \sum_{o}^{n} \frac{U_n}{F+M+nK} e^{-nK(t_c-t_o)} [1 - e^{-(F+M+nK)(t_L-t_c)}] \quad \ldots \quad (9.4)$$

Again this expression may be simplified if t_L is sufficiently large for the last term to be neglected. The the yield is given by

$$Y = FR'W_\infty \sum_{o}^{n} \frac{U_n e^{-nK(t_c-t_o)}}{F+M+nK}$$

or, substituting for R'

$$Y = FRe^{-M(t_c-t_r)} W_\infty \Sigma \frac{U_n e^{-nK(t_c-t_o)}}{F+M+nK} \quad \ldots\ldots\ldots \quad (9.5)$$

Besides the total yield, some other quantities are important. Thus the yield is F times the average biomass of fish in the exploited phase, B', and therefore

$$B' = R'W_\infty \Sigma \frac{U_n e^{-nK(t_c-t_o)}}{F+M+nK} \quad \ldots\ldots\ldots\ldots \quad (9.6)$$

Similarly, the average number in the exploited phase is, from equation (9.2′), dividing the catch in numbers by F

$$N' = \frac{R'}{F+M} = \frac{Re^{-M(t_c-t_r)}}{(F+M)}$$

The average weight of the individual fish in the exploited phase is therefore

$$\bar{W} = \frac{B'}{N'} = \frac{Y}{C} = W_\infty \sum_{o}^{n} \frac{U_n (F+M) e^{-nK(t_c-t_o)}}{F+M+nK}$$

Because the recruitment is unknown and often variable, the yields etc. are normally calculated as yield etc. per recruit.

The steps in calculating the yield directly from equation (9.5) have been set out in the attached work sheets. The first, A, shows a layout for calculating yield for a range of values of fishing mortality, F, selectivity (t_c) being constant. The entries in the box at the top left will be completed from the knowledge of the various parameters in the stock, either using the best estimates available, or, if the knowledge is not so precise, a range of values for natural mortality etc.; a separate sheet is used for each set of possible values. The entries in the top middle deal with the calculations which are the same for all values of F. Below are four pairs of columns, (B) and (C), corresponding to the four terms in the summation of equation (9.5). (For convenience most of the entries, columns etc. have been labelled with letters; when referred to in later column headings they are enclosed in brackets, to avoid confusion with the letters used for mortality coefficients etc. In the second row of each column is shown the formula which will normally be used in computing the entry in that column, the third row shows what the entry represents in terms of the various parameters.)

The other work sheets, B.1 and B.2, are used for calculating the yield for varying selectivities. The first is used to calculate t_c and related quantities from the selectivity, which will normally be defined by the size at first capture l_c. The yield for the range of selectivities and any particular fishing mortality can then be calculated as on sheet B.2, which is nearly the same as work sheet A.

9.2 Other forms of the yield equation

It is possible to reduce the calculations and also to take into account a length-weight relationship other than the cubic, by expressing the yield Y in another form using the incomplete Beta function.

This function, which is usually denoted by $B_x(p, q)$ is defined by the integral

$$\int_0^x y^{p-1}(1-y)^{q-1}\,dy$$

where p, q are positive constants and the upper limit of integration, x, is between 0 and 1. For $x = 1$ the expression is the complete Beta function $B(p, q)$.

To obtain the yield in terms of the Beta function we have, from equation (9.3), for $t_L = \infty$

$$Y = \int_{t_c}^{\infty} FN_t W_t dt$$

where

$$N_t = Re^{-M(t_c - t_r)}\, e^{-(F+M)(t-t_c)}$$

which noting that $t - t_c = (t - t_o) - (t_o - t_c)$ can be written as

$$N_t = Re^{M(t_r - t_o)}\, e^{F(t_c - t_o)}\, e^{-Z(t-t_o)}$$

$$W_t = W_\infty (1 - e^{-K(t-t_o)})^s$$

or if W_∞ is proportional to l^b

$$W_t = W_\infty (1 - e^{-K(t-t_o)})^b$$

Using the transformation

$$y = e^{-K(t-t_o)}$$

and calculating the limits of integration, for the new variable,

$$t = \infty \text{ becomes } y = 0$$

$$\text{and } t = t_c \text{ becomes } y = e^{-K(t_c - t_o)}$$

Also the expression $e^{-K(t_c - t_o)}$, which is equal to $1 - \frac{l_c}{L_\infty}$ will be denoted by $1 - c$. The different factors in the integral then become

$$N_t = Re^{M(t_r - t_o)} (1 - c)^{-F/K} y^{Z/K}$$

$$W_t = W_\infty (1 - y)^b$$

$$dt = \frac{dy}{Ky}$$

The yield in weight, Y, then becomes

$$Y = -\int_{1-c}^{0} FRe^{M(t_r - t_o)}\, W_\infty (1 - c)^{-F/K}\, y^{Z/K} (1 - y)^b \frac{dy}{Ky}$$

or writing $g = \frac{F}{K}$, $\quad m = \frac{M}{K}$

$$Y = RW_\infty e^{M(t_r - t_o)}\, g (1 - c)^{-g} \int_0^{1-c} y^{(m+g-1)} (1 - y)^b\, dy$$

Expressing the integral as an incomplete Beta function this becomes

$$Y = RW_\infty \, e^{M(t_r - t_0)} \, g \, (1 - c)^{-g} \, B_{1-c} \, (m + g \, , b + 1)$$

or if $b = 3$

$$Y = RW_\infty \, e^{M(t_r - t_0)} \, g \, (1 - c)^{-g} \, B_{1-c} \, (m + g \, , 4) \quad \ldots\ldots \quad (9.7)$$

That expression for the yield can be considered in two parts; the first ($RW_\infty \, e^{M(t_r - t_0)}$) does not contain either of the parameters (F or t_c) which depend on the amount or pattern of fishing. This part can therefore be considered as constant in studying the effect on the yield of different patterns of fishing. The second part contains only four parameters, the ratios $m = M/K$, $g = F/K$ and b and c.

Tables of the incomplete Beta function are available (Jones, 1957; Wilimovsky and Wicklung, 1963). Tables of $g \, (1 - c)^g$ have been given by Holt (1957). Thus the yield can be expressed as the product of a constant and two quantities obtainable from the tables.

It should be noted that

$$c = 1 - e^{-K(t_c - t_0)} = \frac{l_c}{L_\infty}$$

i.e. it is the proportion of the total growth in length which is made up before the fish enters the exploited phase. Despite the apparent complexity of the expression for the yield, it is determined by only a few quantities: the proportion of the growth completed when the fish is recruited, and the relative magnitudes of the fishing mortality, the natural mortality, and the growth parameter K.

Since b in fact rarely departs appreciably from 3, equation (9.7) can normally be used. Apart from a constant term, at the beginning, this has only three independent variables, C, g, and m and a function of three variables can be readily tabulated directly. This has been done by Beverton and Holt (1964) explicitly as a function of $\frac{M}{K} \, (= m)$, c and $E\left(= \frac{F}{F+M} = \frac{g}{g+m}\right)$. (Examples of these tables are given in Appendix 1.) They deduced the formula in a slightly different form, but it is a matter of simple mathematics to express their expression (12) for $Y' = Y/[RW_\infty \, e^{M(t_r - t_0)}]$ in terms of c, m and g, i.e.

$$Y' = E \, (1 - c)^{\frac{M}{K}} \sum_{0}^{3} \frac{U_n \, (1 - c)^n}{1 + \frac{nK}{M} \, (1 - E)}$$

$$= g\,(1-c)^{m} \sum_{o}^{3} \frac{U_n\,(1-c)^{n}}{g+m+n}$$

$$= g\,(1-c)^{-\varepsilon} \sum_{o}^{3} \frac{U_n\,(1-c)^{g+m+n}}{g+m+n}$$

which may be shown to be equal to $g\,(1-c)^{-\varepsilon}\,B_{1-c}\,(m+g\,,4)$.

These yield tables have been tabulated for a series of values of $\frac{M}{K}$ from 0.25 to 5.00. For each value of $\frac{M}{K}$, the table of values of Y' (proportional to the yield per recruit) forms the equivalent of a yield isopleth diagram from which the form of the relationship of yield with amount of fishing or size at first capture can be determined very easily. Some care should be taken in interpreting changes on the amount of fishing, since the tabulations are given in terms of $E = \frac{F}{F+M}$ and for large values of E — over 0.5 — quite small changes in E correspond to large changes in F.

Other forms for the yield can be obtained by substituting different formulae for the weight in equation (9.3). In particular, over any moderately short period of time, say t_1 to t_2, growth in weight may be treated as exponential;

$$\text{i.e.}\quad w_t = w_1\, e^{g_1(t-t_1)}\quad t_1 < t < t_2$$

where w_1 is the weight at time t_1.

The growth coefficient g_1 will change according to the interval chosen, generally decreasing with increasing age. Substituting, the yield in weight during the period $t_1 - t_2$ is

$$Y = \int_{t_1}^{t_2} FN_t W_t\, dt$$

$$= \int_{t_1}^{t_2} F\,.\,R' e^{-(F+M)(t_c-t_1)}\, e^{-(F+M)(t-t_1)}\, e^{g_1(t-t_1)}\, w_1\, dt$$

$$Y = FR'\, w_1\, e^{-(F+M)(t_c-t_1)}\, \frac{1}{F+M-g_1}\,(1 - e^{-(F+M-g)(t_2-t_1)})$$

The total yield may then be obtained by summing over the whole life span, using a sufficient number of intervals. By expressing growth in this form, it may be seen that the size (or age) at which the total

mass of a year-class is at its maximum is the size at which g is equal to the natural mortality coefficient M (the " critical size " of Ricker). The greatest yield is then obtained by taking all the year-classes as soon as they reach this size. Where the assumptions of the simple yield equation are not fulfilled (e.g. different growth pattern, parameters not constant, etc.), there is always the possibility to apply the method mentioned in the second paragraph of this section of expressing the yield as the sum of the yields in a large number of small time intervals, within which changes in the size of the individuals and the number of individuals in the stock can be ignored. That is, we approximate to the integral of equation (9.3) by the expression

$$Y = \sum_{1}^{k} F_i N_i W_i \Delta t_i \qquad \text{(see section 2)}$$

where the time interval t_c to t_L has been divided into k short intervals, and

F_i = fishing mortality in the ith period

N_i = numbers present at the beginning of the ith period

W_i = average weight of individuals during the ith period

and Δt_i = duration of the ith period.

F_i may be taken as constant $= F$, or some empirical values can be used if there is evidence that fishing mortality varies with age. Similarly, W_i can be determined from a suitable growth curve, or again empirical data can be used to take into account factors such as seasonal variations on growth, etc.

N_i can be determined from the usual formula

$$N_i = R' e^{-(F+M)t} \quad \text{where} \quad t = \sum_{1}^{i-1} \Delta t_i$$

or from the equations

$$N_1 = R'$$

$$N_{i+1} = N_i - (F_i + M) N_i \Delta t_i$$

The expression of the yield in this form is likely to be particularly useful in any fishery where the assumptions of the simple yield curve are not very closely fulfilled; for instance, very seasonal fisheries, or

fisheries such as those with gill-nets, where the fishing mortality may vary with age. Detailed computer studies have been made for the Pacific salmon fisheries where there are complex regulations involving several gears, and a large number of stocks mixing to a greater or lesser extent.

9.3 Exercises

A. Effects of change in fishing intensity

A.1 *North sea plaice* (75-mm mesh)

Approximate parameter values for North sea plaice, with a 75-mm mesh, are as follows:

$$M = 0.1$$
$$L_\infty = 68.5 \text{ cm}$$
$$W_\infty = 2\,860 \text{ g}$$
$$K = 0.095$$
$$t_0 = -0.8 \text{ year}$$
$$t_r = 3.7 \text{ years}$$
$$t_c = 3.7 \text{ years}$$

(Note that North sea plaice do not move into the main fishing grounds until they are three to four years old so that the size at first capture is independent of mesh size for meshes up to about 100 mm.)

1. Using work sheet A, calculate and plot against fishing mortality coefficient (F), curves of exploited population weight per recruit (B'/R) (proportional to catch per unit effort).

   Yield per recruit $\left(\frac{Y}{R}\right)$. Express this in grammes, and also as a percentage of the present yield (i.e. with $F = 0.5$).

   Exploited population numbers per recruit $\left(\frac{N'}{R}\right)$.

   Catch in numbers per recruit $\left(\frac{C}{R}\right)R$.

   Average weight of fish in catch ($\overline{W}$).

   (Note: Take $F = 0$, 0.02, 0.04, 0.06, 0.08, 0.1, 0.2, 0.5, 1.0.)

2. From the tables of yield functions (Appendix 1) using $\frac{M}{K} = 1$, express the yield per recruit for each value of E in the tables as a percentage of the yield per recruit at the present value of E (take this as 0.8). Plot this value (*a*) against E, and (*b*) against $\frac{F}{M}$.

   (Note: First calculate *c*.) How does curve 2 (*b*) compare with the curve of yield per recruit against effort obtained in 1?

3. Repeat 2 for $\frac{M}{K} = 0.5$ and 1.5.

4. The present estimate of F for North sea plaice is about 0.5. What percentage change in fishing intensity from the present level is needed to obtain the greatest steady yield per recruit? By what percentage does this yield differ from the present level? What effect would this change in intensity have on the catch per unit effort and the mean weight of fish in the catch? How do these answers depend on the magnitude of M?

5. Repeat for 140-mm mesh, given that t_c for this mesh size is 5.5 years.

A. 2. *North sea haddock* (75-mm mesh)

Approximate parameter values for North sea haddock with a 75-mm mesh are as follows:

M	=	0.2
L_∞	=	55 cm
W_∞	=	1 300 g
K	=	0.25
t_0	=	–0.2 year
t_r	=	1.0 year
t_c	=	2.1 years

1. Carry through the exercises A.1, and 2, as detailed above. Note: The present estimate of F for North sea haddock is about 0.8; in the yield tables use $\frac{M}{K} = 0.75$.

2. Repeat with $\frac{M}{K} = 0.50$ and 1.25.

3. Repeat for 100-mm mesh, given that $t_c = 3.3$ years.

B. Effects of change in mesh size

B.1. *North sea plaice* ($F = 0.5$)

1. For mesh sizes above 120 mm, the mean selection length l_c can be calculated directly from the selection factor $(b) = 2.2$. Using work sheets B.1 and B.2, with $F = 0.5$, calculate and plot against mesh size curves of $\frac{B'}{R}$, $\frac{Y}{R}$, $\frac{C}{R}$ and $\overline{W}$. Take $M = 0.1$ and other parameter values as listed in A.1. Express the yield as a percentage of the present yield; i.e. with a mesh of 75 mm. (Note: Take mesh sizes of 120, 160, 180, 200, 220, 240 and 260 mm, and also plot the values for meshes of 75 mm and 140 mm previously calculated for $F = 0.5$.)

2. Use the yield tables for $\frac{M}{K} = 1.0$ to determine the form of the curve of yield per recruit against mesh size. Repeat for $\frac{M}{K} = 0.5$, 1.5 (first calculate E and use nearest value of E in tables).

3. What mesh size is needed to give the greatest steady yield per recruit with this value of F? By what percentage does this yield differ from the present level? What would be the corresponding changes in catch per unit effort and average weight of fish in the catch? How do these answers depend on the magnitude of M?

4. Work through examples 1 - 3 as in B.1 above, but using $F = 0.2$ throughout. Compare your results and conclusions with those for $F = 0.5$.

B.2. *North sea haddock* ($F = 0.8$)

1. The relation between mean selection length l_c and mesh size in haddock can be calculated with a selection factor of 3.2. Using work sheets B.1 and B.2, with $F = 0.8$ throughout, calculate and plot against mesh size curves of $\frac{B'}{R}$, $\frac{Y}{R}$, $\frac{N'}{R}$, $\frac{C}{R}$ and $\overline{W}$. Take parameter values as listed in A.2. (Note: Take mesh sizes of 80, 90, 120, 140, 150, 160. Plot also values previously calculated for meshes of 75 and 100 mm with $F = 0.8$.)

2. Use the yield tables to determine the form of the curve of yield per recruit against mesh size for $\frac{M}{K}$ 0.50, 0.75 and 1.25 (use $E = 0.85$, 0.80, 0.70).

3. What mesh size is needed to give the greatest steady yield per recruit with this value of F? By what percentage does this yield differ from the present level? What would be the corresponding changes in catch per unit effort and average weight of fish in the catch? How do these answers depend on the value of M?

4. Work through examples 1 – 4 as in B.2 above, but using $F = 0.3$ throughout. Compare your results and conclusions with those for $F = 0.8$ and also with those for the North sea plaice.

Known data		
Species		
Mesh size		
M	=	
W_∞	=	(g)
K	=	
t_0	=	(year)
t_c	=	(year)
t_r	=	(year)

$t_c - t_r =$

$M(t_c - t_r) =$

$e^{-M(t_c - t_r)} = \qquad = (M)$

$W_\infty e^{-M(t_c - t_r)} = \qquad = (N)$

$t_c - t_o =$

$K(t_c - t_o) =$

$e^{-K(t_c - t_o)} = \qquad = (D)$

$$(B_n) = (F + M + nK)(C_n) = \frac{U_n e^{-nK(t_c - t_o)}}{F + M + nK}$$

n	$(D)^n$	U_n	(G_n) $U_n(D)^n$
0	1	+1	+1
1		−3	—
2		+3	
3		−1	—

	$n=0$		$n=1$		$n=2$		$n=3$							
(A)	(B_0)	(C_0)	(B_1)	(C_1)	(B_2)	(C_2)	(B_3)	(C_3)	(P)	(Q)	(R)	(S)	(T)	(V)
F	$(A)+M$	$\frac{1}{(B_0)}$	$(A)+M+K$	$\frac{(G_1)}{(B_1)}$	$(A)+M+2K$	$\frac{(G_2)}{(B_2)}$	$(A(+M+3K$	$\frac{(G_3)}{(B_3)}$	$(C_0)+(C_1)+(C_2)+(C_3)$	$(P)\times(N)$	$(Q)\times(A)$	$(C_0)\times(M)$	$(S)\times(A)$	$\frac{(Q)}{(S)}$
				—				—		$\frac{B'}{R}$	$\frac{Y}{R}$	$\frac{N'}{R}$	$\frac{C}{R}$	$\overline{W}$
				—				—						
				—				—						
				—				—						
				—				—						
				—				—						
				—				—						
				—				—						
				—				—						
				—				—						
				—				—						
				—				—						

Work sheet B.1. – Mesh size assessments (1)

Known data		
Species		
F	=	
M	=	
W_∞	=	(g)
L_∞	=	(cm)
K	=	
t_o	=	(year)
t_r	=	(year)
b	=	

Note $(D_n) = e^{-nh(t_c - t_o)}$

$(M) = e^{-M(t_c - t_r)}$

$(N) = W_\infty e^{-M(t_c - t_r)}$

(A)	(B)	(C)	(D_1)	(D_2)	(D_3)	(G)	(H)	(J)	(K)	(L)	(M)	(N)
Mesh size (cm)	$(A) \times b$	$\frac{(B)}{L_\infty}$	$1 - (C)$	$(D_1)^2$	$(D_1)^3$	$-\log_e (D_1)$	$\frac{(G)}{K}$	$(H) + t_o$	$(J) - t_r$	$(K) \times M$	$e^{-(L)}$	$(M) \times W_\infty$
	l_c	$\frac{l_c}{L_\infty}$				$K(t_c - t_o)$	$t_c - t_o$	t_c	$t_c - t_r$	$M(t_c - t_r)$		

Known data		
Species		
F	=	
M	=	
W_∞	=	(g)
K	=	
t_0	=	(year)
t_r	=	(year)
b	=	

Note $(E_n) = U_n e^{-nK(t_c - t_0)}$

$$(C_n) = \frac{U_n e^{-nK(t_c - t_0)}}{F + M + nK}$$

n	(F_w) $F + M + nK$
0	
1	
2	
3	

	$n = 0$		$n = 1$		$n = 2$		$n = 3$							
(A)	(E_0)	(C_0)	(E_1)	(C_1)	(E_2)	(C_2)	(E_3)	(C_3)	(P)	(Q)	(R)	(S)	(T)	(V)
Mesh size (cm)	(D_0)	$\frac{(E_0)}{(F_0)}$	$-3(D_1)$	$\frac{(E_1)}{(F_1)}$	$3(D_2)$	$\frac{(E_2)}{(F_2)}$	$-(D_3)$	$\frac{(E_3)}{(F_3)}$	$(C_0) + (C_1) + (C_2) + (C_3)$	$(P) \times (N)$	$(Q) \times F$	$(C_0) \times (M)$	$(S) \times F$	$\frac{(Q)}{(S)}$
	1			—				—		$\frac{P'}{R}$	$\frac{Y}{R}$	$\frac{N'}{R}$	$\frac{C}{R}$	$\overline{W}$
	1			—				—						
	1			—				—						
	1			—				—						
	1			—				—						
	1			—				—						
	1			—				—						
	1			—				—						
	1			—				—						
	1			—				—						

SECTION 10. SPECIAL ASSESSMENTS

The simple yield equation described in the earlier sections depends for its calculation on fairly complete knowledge of the various parameters (growth, mortality, etc.), and with this information it is possible to estimate the steady yield for any combination of fishing mortality and age at first capture. However, even if, as very often happens, information is far from complete, it is possible to answer certain specific questions, e.g. would a moderate increase in size of first capture increase or decrease the steady yield?

10.1 Catch and effort statistics

If statistics are available for a number of periods in which the effort was kept at a steady level it would clearly be possible to derive a purely empirical relation between fishing effort and steady yield, or catch per unit effort. In most fisheries there are few, if any, long periods of constant fishing effort, and the catch and catch per unit effort in any one year will be related not only to the effort in that year, but to the effort in several preceding years. However, the abundance of a particular year-class which has been in the fishery for say four years (i.e. is of age $t_c + 4$), will be governed by a factor equal to $e^{-(F_0+F_1+F_2+F_3)}$ where F_0, F_1, F_2, F_3 are the fishing mortalities in the previous four years; i.e. its abundance will be the same as if it had been in a fishery with a steady fishing mortality of $\frac{1}{4}(F_0 + F_1 + F_2 + F_3)$. The total catch per unit effort (cpe) of all ages is then related to some weighted mean of the fishing effort in the previous years. If this mean is taken over a period equal to the mean duration of life in the exploited phase (e.g. if the age at recruitment is four years old, and the major part of the catch, in weight, is made up of fish between four and nine years old, the mean duration is about three years), then the relation between this mean effort, $\bar{f}$, and cpe will be close to that between effort and cpe in the steady state. The agreement will in fact be almost exact, not only when the effort has not altered greatly, but also when there has been a steady trend in effort. For instance if effort has been increasing, then the older ages will be over-abundant, having had an average fishing effort on them less

than $\bar{f}$, while the younger ages will be too scarce, having experienced an average effort greater than $\bar{f}$.

This relation is best expressed graphically by plotting cpe against $\bar{f}$; the best fit is usually not a straight line, but a curve concave upward, for instance the curves for plaice or cod at Iceland (Gulland, 1961b). From this curve, giving the steady state relation between cpe and effort, the corresponding relation between catch and effort can be determined at once by multiplication.

This approach is very close to the constant parameter model of the complete yield curve, in which density-dependent effects are ignored, as most of these take effect over longer periods of time. For instance, in the example above, if recruitment is affected, the present stock is the offspring of the stock on the average six to seven years earlier, which in turn was determined by the fishing over the previous three years or more.

The major advantage of this method is that it requires easily obtainable data; total catch is usually known, and effort or cpe data are usually among the earliest semiscientific data to be collected. If there are errors in the effort data (the most likely being uncorrected trends, such as increased efficiency) these will affect both x and y values in the plotting, and tend to displace the points along lines of the form $y = a/x$. The displacement is in a similar direction as the general form of the expected regression, so that it appears that errors in effort measurement will not distort the estimate of the relation between cpe and effort, but may make the statistical significance of the fit greater than it really is. If the series of data is long enough the effect of changes other than simply of total effort may be studied. Thus if there has been a change in fishing practice, e.g. an increase of mesh size, in the middle of the series, then, if this has had a significant effect on the stock, two different regressions of cpe on effort for the periods before and after the change could be determined.

10.2 Schaefer's model

Another method of analysis depending chiefly on catch and effort data is that of Schaefer, 1954, 1957. The population biomass, B, is considered as a single entity, which would, if fishing were not present, increase at a rate determined by its size, i.e.

$$\frac{dB}{dt} = f(B)$$

where $f(B)$ is some function of B, being zero when $B = 0$, and when B is at its maximum B_M, and $f(B)$ will have a maximum at some intermediate value of B.

Therefore, when fishing is present

$$\frac{dB}{dt} = f(B) - Y = f(B) - FB \text{ where } Y = \text{catch.}$$

Clearly the population will remain constant if $Y = f(B)$, so that at any population size there will be a certain equilibrium catch, and this will be a maximum when $f(B)$ is a maximum.

The form of $f(B)$ may be determined from data on catch and effort, provided there is also some information (e.g. on tagging) from which catch per unit effort figures can be converted into absolute terms, i.e. if the coefficient q (k_2 in Schaefer's notation) is known. Thus if the values of catch per unit effort are known at the beginning and end of a year

$$\text{initial population} = B_1 = \frac{1}{q}\left(\frac{y}{f}\right)_1$$

$$\text{final population} = B_2 = \frac{1}{q}\left(\frac{y}{f}\right)_2$$

$$\text{mean population} = \bar{B} = \frac{1}{2}(B_1 + B_2)$$

then $B_2 - B_1 =$ change in population $= f(\bar{B}) - Y$ or $f(\bar{B}) = B_2 - B_1 + Y$ where Y is the catch during the year.

Usually the catch per unit effort will not be known at the beginning of the year, but as the mean value over the year. The catch per unit effort at the beginning of the year may instead be estimated as the mean of the average catches per unit effort during the preceding and subsequent 12 months. A pair of values of $f(\bar{B})$ and $\bar{B}$ can therefore be obtained for each year, and by plotting one against the other the relation between equilibrium catch and stock size may be established. The fitting may be made more quickly if some form for $f(B)$ is assumed, for instance the relation

$$f(B) = aB(B_M - B)$$

which plotted against B gives a parabola. This form of curve is best fitted by plotting $\frac{f(B)}{B}$ against B, which gives a straight line. This method of analysis has much in common with that of the previous section. Both attempt to obtain the equilibrium relation between catch and effort (or one of its transformations) by suitable adjustment of data

from a changing fishery — one by taking into account effort data in earlier years, and the other, changes in the catch per unit effort. This model has apparent advantages of simplicity and only a small demand on data. Also it gives the impression of being more closely related to the realities of natural population than the analytic model of the earlier section, at least when for the latter no account is taken of possible changes in the parameters of growth, mortality and recruitment, related to changes in the abundance of the population.

These advantages are, however, mainly superficial. The analytic model can be modified to take into account the complexities of any natural population whereas the Schaefer model is very difficult to modify. Also the natural rate of increase of a population is not determined uniquely and solely by the population biomass at one time. The recruitment is determined (apart from environmental factors) by the adult stock some time in the past, often several years. The increase in population biomass due to growth either absolutely or as a percentage of the present biomass depends as much if not more on the age structure of the population than on its total biomass. To take these effects into account the use of some form of analytic model is required.

10.3 Changes in selectivity

The simplest and perhaps the most important question concerning the effect of a possible change in selectivity is whether the change will result in an increase or decrease in the average catch. This can be done, following Allen (1953), by comparing the weight of the individual fish of the size it is proposed to release, with the probability of their being caught again later and their average weight when caught. That is, if

W_c = weight of individual fish at the mean selection length

$\bar{W}$ = mean weight of fish in the catch larger than W_c

then the catch will be increased by releasing the fish if $E \times \bar{W} > W_c$ where E = probability of a released fish being caught later $= \frac{F}{F+M}$ if the fishing and natural mortalities are constant. Or, in terms of the ratio of fishing to total mortality, the catch will be increased if $E > \frac{W_c}{\bar{W}}$. The right-hand side of this inequality can be readily calculated from simple observations of the size composition of the catches.

Some more detailed effects of changes in selectivity can be also determined from a knowledge of the size composition of the landings

(see Gulland, 1961a, 1964a). Thus, immediately following a change in gear there will be no change in the stock, and the numbers of any given size, l, of fish landed by the new gear (e.g. increased mesh size) will be given by

$$ {}_lN_k = {}_lN_1 \frac{{}_lr_2}{{}_lr_1} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (10.1) $$

where

$ {}_lN_1 $ = numbers landed by old gear

$ {}_lN_k $ = numbers landed by new gear

$ {}_lr_1 $ = proportion retained by old gear

$ {}_lr_2 $ = proportion retained by new gear.

If also $ {}_lW $ = average weight of fish of length l then the total weight W_1, caught with the old gear, is given by

$$ W_1 = \Sigma\, {}_lW\, {}_lN_1 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (10.2) $$

and weight caught with the new gear, W_k, is

$$ W_k = \Sigma\, {}_lW\, {}_lN_k \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (10.3) $$

Also the total numbers landed by the old gear, N_1, and retained by the new gear, N_k, can be written

$$ N_1 = \Sigma\, {}_lN_1, \text{ and } N_k = \Sigma\, {}_lN_k. $$

(If the average weights $ {}_lW $ and the relevant numbers are arranged as parallel columns these calculations of sums of products are simple to carry out on most calculating machines.) The actual immediate change in landings can be expressed as a proportion L of the initial landings, where

$$ L = \frac{W_1 - W_k}{W_1} $$

When an increase in mean selection length takes place the fish released by the new gear, but which could have been caught by the old gear, will grow, and after a time reach the size at which they will be retained by the new gear, and the catches will increase.

The number, N_R, of fish released, which would previously have been landed, will be equal to $N_1 - N_k$. If quantities of small fish are caught

and discarded at sea, and not landed, the total numbers released will be greater than the reduction in the landings, and may be calculated as

$$N_R = \sum_l {}_lN_c \left(1 - \frac{l_{r_2}}{l_{r_1}}\right) \quad \ldots\ldots\ldots\ldots\ldots\ldots (10.4)$$

where ${}_lN_c$ are the numbers of fish of length l caught by the old gear including discards. Of these fish a number $N^1{}_R = N_R e^{-MT}$ will survive to ${}_2t_c$, the mean age of first capture with the new mesh, where T is the difference between ${}_2t_c$ and the average age of the fish released. In turn, of these fish a number $EN^1{}_R$ will ultimately be caught, where E is the exploitation rate $\left(= \frac{F}{F+M} \text{ when the mortalities are constant}\right)$. As all the mortalities etc. for fish greater than ${}_2l_c$ are unchanged, the size distribution of these fish will be the same as that of the N_k fish, so that after a period the catches with the new gear will be increased by a proportion Q, when

$$Q = \frac{EN^1{}_R}{N_k} \quad \ldots\ldots\ldots\ldots\ldots\ldots (10.5)$$

Thus the long-term landings, W_2, will be given by

$$W_2 = W_1 (1 - L)\ (1 + Q) \quad \ldots\ldots\ldots\ldots\ldots\ldots (10.6)$$

This level of landings may not be reached until several years after the change in selectivity. It will only be complete after a period, equal to the life span of the fish in the fishery, has elapsed since the change in selectivity, although it will be close to this value at a rather earlier date. The catches in the interim period can be estimated as follows. In order to estimate the landings at time t', suppose that fish of the size released will have grown to a certain length l'. Then, at a time t' after the change in mesh size, the fish larger than l' will have been fished by the old mesh when they were of a size in the selection range, so that the stock and catches of these fish will be nearly unaffected by the change, and the weight caught of fish length $l > l'$ would be ${}_lW_lN_R$. Fish smaller than length l' would have been under the influence of the new mesh during their life in the exploited phase so the stock and catches of these sizes could be the same as in the long-term equilibrium state with the new mesh, and the weight caught of fish length $l < l'$ would be $(1 + Q)\,{}_lW_lN_R$. The total weight caught will be W', given by

$$W' = \sum_0^{l'} (1 + Q)\,{}_lW_lN_k + \sum_{l'}^{\infty} {}_lW_lN_k$$

i.e.

$$W' = Q \sum_{o}^{l'} {}_{l}w_{l}N_{k} + W_{k} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (10.7)$$

The method can be extended to stocks fished with more than one gear, some of which may not change their selectivities. Here equations (10.1) and (10.3) are applied separately to each fleet to find the immediate effects. The factor Q will be the same for all, and is given from the extension of equation (10.5) in the form

$$Q = \frac{E \Sigma N'_R}{\Sigma N_k} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (10.8)$$

where the summation of N_k includes the fish caught by all gears (omitting any fish, caught by gears whose selectivity does not change, smaller than the new selection length), but the summation of N_R will, of course, only include gears whose selectivity changes. The calculations necessary to assess the results of a mesh change when two gears, possibly catching different sizes of fish, are operating are set out in the work sheet on p. 127.

10.4 Interacting fisheries

The above methods may also be used to study the interaction of different fisheries, particularly of a fishery (A) principally for one species (e.g. herring) which incidentally catches young fish of another species (e.g. haddock), which, when older, is itself the principal object of some other fishery (B).

The steps are again

(*a*) Calculate the number of fish caught by fleet (A), or the extra number being caught compared with what would have been caught supposing fleet (A) was complying with some desired regulation $(= N)$.

(*b*) Calculate the reduced numbers of these which will survive until the age of first capture of fleet (B) $(= N^1)$.

(*c*) Compare the numbers of these $= EN^1$, which would be caught, with the present catch, C, of fleet (B). Then the increase in the catches of fleet (B) which would take place if fleet (A) stopped fishing, is, as a proportion of the present catch: EN^1/C. The same result may be obtained by comparing N^1 with the numbers of fish recruiting to fleet (B), which is $\frac{C}{E}$ (see International Council for the Exploration of the Sea, 1960).

WORK SHEET C. – Assessment of changes in selectivity (for two gears with different size compositions of their catches)

Part 1. – Immediate effects

(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(F)	(G)	(H)
				$\frac{(D)}{(C)}$	$(F) \times (1-(E))$	$(F) \times (E)$		$(F) \times (F) \times (1-(E))$	$(F) \times (F) \times (E)$	
		Proportion retained			Numbers for gear A			Numbers for gear B		
l	${}_lW$	${}_lr_1$	${}_lr_2$	$\frac{{}_lr_2}{{}_lr_1}$	${}_lN_1$	${}_lN_R$	${}_lN_K$	${}_lN_1$	${}_lN_R$	${}_lN_K$
				$\Sigma\, {}_lN$	—	—	—	—	—	—
				$\Sigma\, {}_lN \times {}_lW$	—	—	—	—	—	—
				$L = \frac{W_R}{W_1}$		—			—	

Part 2. – Long-term effects

N_R: Number released — N_K: Number in catches immediately after change

Gear A — Gear A

Gear B — Gear B

Discards: _____ — Nonregulatory gears: _____

Total: _____ — Total: _____

$$\frac{N_R}{N_K} = \text{_____}$$

$T =$ — $MT =$

$e^{-MT} =$ — $\frac{N_R}{N_K} e^{-MT}$

			Gear A		Gear B	
E	Q	$1+Q$	$(1-L)(1+Q)$	G	$(1-L)(1+Q)$	G

$$Q = E \frac{N_R}{N_K} e^{-MT} \qquad G = 1-(1-L)(1+Q)$$

10.5 Exercises

1. The table below gives the catch per unit effort (catch, in tons, per 1 000 ton-hours' fishing by United Kingdom trawlers) and the total catch, in thousands of tons, of cod and haddock, at Iceland.

Year	Total catch		Catch/Effort		Year	Total catch		Catch/Effort	
	Cod	Haddock	Cod	Haddock		Cod	Haddock	Cod	Haddock
1906	105	35	0.97	0.55	1936	280	25	1.14	0.14
1907	115	30	1.03	0.49	1937	295	25	1.39	0.11
1908	125	31	1.20	0.54	1938	305	24	1.11	0.16
1909	115	28	1.05	0.57	1939	198	13		
1910	135	30	1.12	0.56	1940	149	20		
1911	155	31	1.26	0.58	1941	158	15		
1912	160	28	1.20	0.47	1942	176	17		
1913	180	26	1.27	0.38	1943	189	13		
					1944	220	12		
1919	130	35	1.41	1.01	1945	216	14		
1920	190	53	1.39	0.70	1946	237	28	1.84	0.63
1921	175	37	1.16	0.58	1947	246	33	1.46	0.42
1922	220	40	1.27	0.61	1948	293	52	1.27	0.32
1923	220	38	1.09	0.44	1949	315	66	1.17	0.37
1924	300	38	1.09	0.30	1950	321	60	0.98	0.24
1925	320	35	1.28	0.31	1951	327	54	0.94	0.19
1926	295	37	1.09	0.32	1952	392	45	0.91	0.18
1927	340	54	0.99	0.38	1953	515	53	1.11	0.18
1928	360	57	0.88	0.34	1954	546	62	1.01	0.17
1929	390	54	0.83	0.29	1955	537	64	1.04	0.21
1930	490	49	1.10	0.28	1956	482	62	1.02	0.19
1931	475	40	1.09	0.21	1957	453	76	0.81	0.16
1932	480	32	1.34	0.19	1958	511	70	0.80	0.14
1933	510	26	1.28	0.14	1959	454	64	0.68	0.18
1934	480	26	1.14	0.14	1960			0.64	0.18
1935	400	27	1.16	0.14					

(*a*) Calculate the total fishing effort, in United Kingdom units, on cod and on haddock each year.

(*b*) If the average duration of life in the fishery is two years for haddock and three for cod, relate the stock abundance to the past fishing effort. Is there any suggestion that either of these relations has changed? In particular, examine the haddock curve for the years since 1950, when a larger mesh was introduced and trawling was banned in certain areas, including some nursery areas.

2. The table below gives data on catches and catch per unit effort of blue whales in the Antarctic. Taking alternative values of the population size corresponding to a catch per unit effort of 1.00 as 20 000 and 30 000 whales, calculate the change in population size each year, and hence the sustainable yield each year. Plot this against population size in that year, and that five years earlier (assuming

Year	Total catch	Catch per unit effort
1925/26	4 697	3.30
1926/27	6 545	3.76
1927/28	8 334	4.39
1928/29	12 734	4.49
1929/30	17 898	3.13
1930/31	29 410	3.71
1931/32	6 488	4.83
1932/33	18 890	4.61
1933/34	17 349	4.76
1934/35	16 500	3.46
1935/36	17 731	3.96
1936/37	14 304	2.83
1937/38	14 923	2.00
1938/39	14 081	1.77
1939/40	11 480	
1940/41	4 943	
1941/42	59	
1942/43	125	
1943/44	339	
1944/45	1 042	
1945/46	3 606	1.36
1946/47	9 192	1.85
1947/48	6 908	1.12
1948/49	7 625	0.98
1949/50	6 182	0.80
1950/51	7 048	0.81
1951/52	5 130	0.63
1952/53	3 870	0.44
1953/54	2 697	0.42
1954/55	2 176	0.31
1955/56	1 614	0.37
1956/57	1 512	0.27
1957/58	1 690	0.28
1958/59	1 187	0.18
1959/60	1 228	0.14
1960/61	587[1]	0.105
1961/62	639[1]	0.093

[1] Omitting pygmy blue whales

blue whales recruit to the exploited stock at five years of age). How may the catch data for the years 1939-46 be used? What is the maximum sustainable yield, and at what population size is it taken?

3. Data for the United Kingdom trawl fishery for haddock at the Faroe islands are given below, showing the numbers landed in each 5-cm-length group, their average weight, and the proportion of each group retained by a 90-mm and a 120-mm mesh.

Length	Average weight	Percentage retained		Numbers landed
cm	*g*	*90 mm*	*120 mm*	*Thousand*
25–29	160	50	3	8
30–34	260	80	16	314
35–39	420	98	41	1 084
40–44	630	100	72	1 409
45–49	880	100	94	1 370
50–54	1 190	100	100	952
55–59	1 570	100	100	465
60–64	1 760	100	100	255
65–69	2 530	100	100	124
70–74	3 100	100	100	73
75–79	3 800	100	100	30
80+	4 600	100	100	9

(*a*) What is the present total weight landed?

(*b*) If the present mesh was 90 mm, what would be the reduction in catch (as a percentage) immediately following an increase to 120 mm?

(*c*) If it takes an average of six months for the fish released to grow to the size of first capture of the 120-mm mesh, what would be the long-term effect of an increase of mesh to mm, assuming that there is no other fishery, and that the natural mortality of fish in the selection size is 0.2, and $E\,(= F/F + M) = 0.5$?

(*d*) What would be the long-term effects on both fleets (as percentages, and actual weights) if there was also a line fishery operating, taking an average annual catch of five million fish weighing 6 000 tons, and $E = 0.7$? Assume all line-caught fish are larger than the selection size of the 120-mm mesh.

(*e*) What would be the effects if the trawlers discarded 30 percent of the catch (by numbers), and these fish were all small enough to escape through a 120-mm mesh? (Let T = one year, say.)

4. The average annual catch of haddock by trawlers fishing for herring in 1954-56 was as follows:

Size	Weight caught	Weight landed	Fish
	Tons		*Million*
Under 24 cm	2 500	—	25
24-27 cm	6 000	—	45
Over 27 cm	23 500	14 000	[illegible]
Total	32 000	14 000	150

The fishery for haddock lands on an average 70 000 tons per year of fish whose average weight is 330 g.
If the herring trawlers were to use a mesh of the minimum size for demersal fishing, what would be the effect on the haddock catches assuming:

(*a*) The legal mesh releases all haddock less than 24 cm.

(*b*) In the haddock fishery some 100 million fish over 24 cm are caught, but are rejected as being below the marketable size of 27 cm.

(*c*) The fish below 24 cm which would be released by a larger mesh take an average of six months to grow to 24 cm, during which time they would suffer a natural mortality of 0.2.

(*d*) $E = F/(F + M) = 0.8$ (where F includes all forms of fishing).

SECTION 11. CHANGES IN THE PARAMETERS

In the previous section all the parameters (growth, mortality, etc.) have been assumed to be constant, except for the explicit changes in the fishing mortality or the age at first capture. In fact changes in all are possible, and some, e.g. the annual recruitment, can vary very widely. These changes may be the result, directly or indirectly, of changes in the abundance of stock (and hence possibly influenced by fishing), or be independent of the stock, and the result of changes in the environment — amount of food, etc. The latter can be divided, according to the effect produced, into two types of change. First there are those that alter the shape of the yield curves, so that the results of, for example, an increase of mesh size may be quantitatively different, and secondly those that only affect the height of the yield curve, and which therefore for many purposes can be neglected.

The best example of the second is the big variation that can occur, independent of changes in adult spawning stock, in the strength of successive year-classes of many fish, e.g. in haddock, herring, etc. Calculations omitting data on year-class change may suggest that an increase of mean size from the present (say 100 mm to 110 mm) may increase the steady yield by say 5 percent. From this it need not be true that, if the mesh were increased, the yield in some particular future year would be exactly 5 percent greater than the present, because the year-classes then being fished may be of different strength. What is true (if the calculations are correct) is that the yield would be 5 percent above what it would have been if the old, 100-mm, mesh had been in use. For many practical questions (e.g. is a change from 100 to 110 mm advisable?) the differences due to change in recruitment are not of significance. For this reason, and because, as may be seen in the previous sections, that is the form in which the expression for the yield is often obtained, many assessments are stated in the form of yield per recruit. An exception is when the amount of fishing depends critically on the strength of the year-classes in the fishery, there being little or no fishing when year-classes are weak. A good example is the haddock fishery on Saint Pierre bank, where there was a big fishery on the outstanding 1949 year-class between 1953 and 1957, with little before or since.

Growth changes can have an effect on the shape of the yield curve, particularly that relating yield to size at first capture. In a heavily fished stock the maximum yield may be obtained with a size at first cap-

ture, l_c, not far below the maximum size, L_∞, but if there is a change in growth with a new and smaller L_∞, not many fish may survive to l_c and the yield with that value of l_c may be small.

11.1 Density-dependent effects

While some changes in the environment may mean that the shape of the yield curves in the future will be different from those under the present conditions, density-dependent effects can mean that the real yield curve is different from that calculated on the assumption of constant parameters. If the stock increases, e.g. following a reduction in fishing, the likely effects are that natural mortality will increase, and the growth decrease, but that the recruitment will increase. These effects act in opposite directions, the first two reducing the yield at high stock levels (i.e. at low fishing intensities, or with a large mesh size), but the last increasing the yield under these conditions of fishing. In a heavily fished stock, where reduced fishing or increased mesh size would be expected to increase the yield, density-dependent mortality and growth have a damping effect, tending to make the yield curve flat, but the recruitment effect will exaggerate the changes. Density-dependent recruitment is therefore rather the more critical effect.

If a relation can be established between any particular parameter and stock abundance, then it is possible to incorporate this into the simple yield equation. Usually it is not possible to produce an explicit mathematical expression for the stock or yield when a parameter changes with stock density, but estimates of stock and yield may be obtained for any given conditions of fishing effort, etc. by successive approximations. For instance, if natural mortality is proportional to stock abundance, then to calculate the yield and stock at say twice the present fishing, we can take a first estimate of a halved stock, and therefore halved M; using this value of M in the equations will give a better estimate of stock, hence of M, which in turn can be used to provide better estimates.

In fact it is often impossible to determine the density effects on the various parameters, especially of natural mortality, and it is probably best to take certain likely relations and see how these affect the shape of the yield curve (see Beverton and Holt, 1957, section 18).

In studying the effect on recruitment two quantities may be related to stock size — the recruitment, i.e. the absolute number of young fish produced from a given stock, and the survival, i.e. the numbers of young per million eggs. If, as is sometimes assumed, recruitment is constant, at least over the range of probable stock sizes, use of both relations may therefore show whether a nonsignificant (in the statistical sense) relation between stock and recruitment is caused by a real and significant (in the biological and practical sense) change in recruitment with

stock size which is obscured by variation in the data, or whether the average recruitment is really constant. The second alternative should be detectable by a relation between survival and recruitment.

11.2 Exercises

1. The spawning stock of North sea plaice may be estimated as the catch by weight per 100 hours' fishing by United Kingdom trawlers, and the recruitment as the catch in numbers per hours of four-year-old fish four years later. Available data for the past years are given below (from Beverton, 1962).

Year	Stock	Recruitment	Yea	Stock	Recruitment
	cwt			*cwt*	
1926	16	18	1945	150	33
1927	15	28	1946	76	32
1928	16	61	1947	54	45
1929	16	36	1948	44	22
1930	17	27	1949	35	20
1931	16	18	1950	33	23
1932	16	28	1951	31	9
			1952	32	22
1943	120	18			
1944	140	16			

Assuming that the number of eggs produced is proportional to stock size, calculate an index of survival from eggs to recruitment. What is the relation (*a*) between stock and recruitment; (*b*) between stock and survival?

SECTION 12. FINAL EXERCISES

(Note: This set of exercises has been constructed to illustrate how the calculations in all the previous sections may be combined to provide assessments and practical advice in the management of a fishery.)

The following data were obtained from the trawl fishery for chafer fish in the Round sea.

The data have been grouped into three periods, on the basis of the different levels of the fishing effort in three periods.

1. Catches. The catches are given in thousand tons, numbers in millions, effort in thousand hours' fishing.

Year		Catch		Effort
Period 1		*Thousand tons*	*Millions*	*Thousand hours*
	1932	82.2	118.5	30
	1933	109.4	143.2	40
	1934	66.7	82.0	24
	1935	108.0	124.9	45
	1936	45.0	51.4	25
	1937	111.3	155.5	46
	1938	79.1	105.3	35
Period 2				
	1950	136.0	190.1	91
	1951	102.7	144.6	72
	1952	141.1	217.1	84
	1953	122.2	179.2	75
	1954	81.1	110.9	62
	1955	126.0	191.4	81
	1956	164.0	241.7	103
Period 3				
	1961	128.8	177.2	116
	1962	170.4	270.3	142
	1963	158.4	256.0	138
	1964	122.1	188.7	132
	1965	155.0	267.3	125
	1966	135.9	216.3	128
	1967	143.9	249.4	115

By plotting the data on total catch and catch per effort, against the appropriate effort, can you obtain a preliminary conclusion on the state of the fishing and the expected effect of a change in effort?

2. The age compositions, obtained from age-length keys based on otolith age readings, and the annual length compositions, are (in percentages):

Year \ Age	3	4	5	6	7
	Percentage				
1932	35.4	49.3	10.0	3.9	1.4
1933	34.5	24.3	32.7	6.5	2.0
1934	32.4	25.2	16.2	21.9	4.3
1935	27.9	25.0	17.5	12.5	17.1
1936	23.3	25.0	22.8	17.8	11.1
1937	55.8	13.2	12.4	11.2	7.4
1938	35.4	39.8	8.0	8.8	8.0
1950	40.5	34.1	16.0	6.4	3.0
1951	49.0	21.2	17.5	8.8	3.5
1952	60.7	20.2	8.6	7.1	3.3
1953	49.1	31.0	10.7	4.9	4.3
1954	38.2	32.4	19.9	6.9	2.7
1955	61.7	14.1	13.5	8.0	2.6
1956	50.9	30.0	9.4	5.8	4.1
1961	31.5	48.2	9.5	7.9	2.7
1962	66.9	10.8	16.4	3.2	2.6
1963	62.6	25.9	3.9	6.4	1.2
1964	54.8	28.8	11.7	1.9	2.8
1965	73.7	15.0	7.7	3.1	0.5
1966	57.0	31.5	6.5	3.5	1.5
1967	74.1	15.0	8.6	1.6	0.8

(*a*) Estimate the total mortality coefficient (Z) for each of the three periods. Determine the coefficient of natural mortality (M), using these values of Z and the average effort in each of the three periods.

(*b*) Estimate also the coefficient of fishing mortality F.

3. The relation between age and length in the chafer fish is the following:

$l_1 = 10$ cm; $l_2 = 22$ cm; $l_3 = 33$ cm; $l_4 = 38$ cm; $l_5 = 45$ cm; $l_6 = 48$ cm; $l_7 = 50$ cm; $l_8 = 52$ cm.

Fit a von Bertalanffy curve to these observations, and estimate the growth parameters. $W = 0.01\, l^3$

4. Selectivity experiments with a covered cod-end and mesh size of 100 mm gave the following results:

Length	Number of fish	
	In cod-end	In cover
..... *cm*		
29	0	510
30	30	623
31	82	728
32	151	855
33	554	555
34	631	276
35	778	85
36	698	12
37	500	0

Determine the mean selection length, and the selection factor. Note that the lengths were recorded to the cm below.

5. In recent years (i.e. in the third period under consideration) the mesh size used in the fishery for chafer fish was 100 mm. Make use of the yield tables for the following questions:

   (*a*) Is it possible to obtain a greater catch using this mesh size and increasing the fishing effort?

   (*b*) What effort would give the maximum yield for this mesh size, and what is the yield at this level of effort?

   (*c*) What would be the effect on the yield of an increase in the mesh size from 100 to 110 mm, keeping the effort at the level of the third period?

   (*d*) What mesh size would give the maximum yield for this effort, and what would be this yield?

Appendix 1

YIELD TABLES FOR M/K = 0.50,

$M/K = 0.50$

E	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50
c										
98	006927	013843	020748	027640	034517	041379	048223	055046	061845	068618
96	009596	019164	028699	038199	047659	057075	066440	075748	084991	094158
94	011514	022977	034382	045722	056991	068179	079276	090270	101145	111886
92	013027	025976	038837	051600	064255	076788	089183	101421	113482	125338
90	014272	028436	042479	056389	070149	083741	097143	110331	123275	135938
88	015322	030503	045529	060381	075040	089481	103678	117598	131203	144447
86	016220	032266	048119	063757	079155	094284	109110	123593	137686	151334
84	016997	033785	050340	066637	082646	098331	113652	128563	143006	156915
82	017674	035102	052257	069108	085621	101754	117462	132687	147366	161420
80	018267	036249	053916	071234	088162	104653	120654	136101	150920	165022
78	018787	037251	055357	073066	090333	107105	123321	138910	153787	167855
76	019245	038127	056608	074644	092185	109171	125535	141198	156066	170030
74	019648	038894	057694	076001	093759	110902	127356	143034	157833	171635
72	020004	039565	058636	077165	095089	112340	128834	144476	159157	172744
70	020317	040151	059450	078157	096206	113520	130010	145574	160092	173423
68	020593	040662	060151	078999	097134	114473	130922	146369	160687	173724
66	020836	041106	060752	079708	097895	115226	131600	146898	160983	173696
64	021049	041491	061264	080297	098508	115802	132072	147192	161018	173381
62	021235	041823	061697	080781	098989	116220	132362	147280	160824	172814
60	021398	042107	062059	081171	099353	116500	132491	147187	160428	172028
58	021539	042350	062357	081477	099614	116656	132479	146935	159857	171052
56	021661	042554	062599	081709	099783	116704	132342	146543	159134	169912
54	021767	042724	062791	081875	099870	116656	132095	146030	158278	168631
52	021856	042864	062939	081982	099886	116524	131754	145411	157308	167230
50	021933	042978	063046	082038	099839	116318	131329	144701	156241	165728
48	021997	043067	063119	082048	099736	116048	130832	143914	155092	164142
46	022050	043135	063161	082018	099585	115723	130274	143060	153875	162487
44	022094	043185	063175	081952	099391	115349	129664	142151	152601	160778
42	022129	043218	063165	081857	099162	114935	129009	141196	151282	159026
40	022156	043236	063135	081734	098902	114487	128318	140205	149928	157243
38	022177	043242	063086	081590	098616	114010	127598	139185	148548	155440
36	022192	043236	063022	081426	098307	113509	126855	138143	147150	153626
34	022202	043222	062945	081246	097982	112991	126093	137086	145742	151808
32	022208	043199	062857	081053	097641	112458	125320	136020	144331	149995
30	022210	043169	062760	080850	097290	111915	124538	134951	142921	148193
28	022209	043134	062655	080638	096931	111365	123753	133882	141519	146408
26	022205	043094	062545	080420	096566	110812	122967	132818	140130	144646
24	022199	043050	062430	080197	096198	110258	122184	131762	138756	142909
22	022191	043004	062311	079972	095829	109705	121407	130718	137403	141203
20	022182	042955	062190	079745	095460	109156	120638	129689	136072	139531
18	022171	042904	062069	079519	095093	108613	119880	128677	134766	*137894
16	022160	042853	061946	079293	094730	108077	119134	127683	133488	*136297
14	022148	042801	061824	079069	094371	107549	118401	126710	132240	*134739
12	022136	042749	061703	078848	094018	107030	117683	125759	131021	*133223
10	022124	042697	061583	078631	093672	106522	116981	124830	129834	*131748
00	022063	042450	061016	077605	092045	104150	113716	120530	124367	*125000
F/M	0.0526	0.111	0.177	0.250	0.333	0.429	0.539	0.667	0.818	1.00
F/K	0.0260	0.056	0.088	0.130	0.170	0.210	0.270	0.330	0.410	0.50

For notes, see end of table.

1.00 AND 1.75 [1]

$M/K = 0.50$

0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95	1.00	E
										c
075359	082063	088725	095336	101887	108363	114750	121024	127156	*133105	98
103239	112219	121081	129802	138356	146708	154812	162610	170023	*176947	96
122471	132874	143064	153003	162642	171921	180760	189057	196679	*203451	94
136959	148306	159333	169983	180184	189845	198852	207056	214268	*220246	92
148280	160247	171778	182794	193199	202873	211663	219375	225764	*230530	90
157277	169625	181412	192539	202886	212300	220591	227522	232797	*236069	88
164469	177012	188864	199907	209992	218938	226518	232453	236404	*237990	86
170212	182800	194565	205365	215028	223343	230049	234827	*237305	237082	84
174759	187271	198824	209255	218369	225924	231628	235129	*236029	233926	82
178303	190638	201877	211837	220297	226991	231596	*233733	232986	228973	80
180997	193071	203911	213314	221038	226790	230222	*230934	228502	222585	78
182961	194704	205075	213853	220774	225522	*227727	226974	222845	215053	76
184296	195649	205493	213589	219654	223351	*224293	222055	216234	206625	74
185086	195999	205268	212638	217806	*220418	220073	216344	208858	197504	72
185402	195834	204490	211097	215337	*216841	215199	209988	200875	187869	70
185306	195224	203234	209051	212341	*212724	209783	203111	192425	177870	68
184850	194226	201567	206573	*208899	208156	203926	195823	183628	167638	66
184083	192894	199546	203727	*205082	203215	197714	188219	174587	157286	64
183044	191273	197223	200571	*200953	197971	191223	180383	165395	146915	62
181770	189405	194643	*197154	196567	192486	184521	172389	156132	136610	60
180294	187325	191847	*193521	191975	186813	177667	164303	146871	126447	58
178645	185067	188870	*189714	187220	181003	170716	156183	137673	116490	56
176849	182659	185747	*185767	182342	175097	163715	148081	128594	106797	54
174930	180127	*182505	181712	177378	169137	156706	140043	119682	097416	52
172909	177497	*179171	177580	172357	163155	149728	132109	110980	088388	50
170804	174788	*175769	173396	167310	157184	142813	124315	102524	079749	48
168634	172020	*172319	169183	162262	151251	135992	116692	094346	071527	46
166413	*169210	168842	164963	157236	145381	129292	109268	086474	063746	44
164157	*166375	165354	160755	152252	139595	122734	102067	078931	056424	42
161877	*163528	161871	156574	147328	133915	116341	095109	071734	049574	40
159585	*160681	158407	152437	142481	128355	110128	088412	064900	043206	38
157292	*157847	154973	148357	137725	122932	104112	081989	058441	037325	36
155006	*155035	151582	144345	133073	117658	098305	075854	052365	031931	34
*152736	152254	148243	140411	128534	112544	092718	070013	046677	027021	32
*150489	149512	144963	136566	124119	107600	087358	064475	041381	022590	30
*148272	146817	141752	132815	119834	102831	082233	059244	036476	018627	28
*146089	144173	138614	129167	115686	098245	077347	054321	031959	015119	26
*143947	141586	135555	125625	111681	093846	072704	049708	027826	012051	24
*141848	139061	132579	122194	107822	089636	068303	045402	024069	009404	22
*139797	136600	129690	118878	104111	085617	064145	041399	020678	007155	20
137796	134208	126891	115672	100551	081790	060229	037695	017641	005281	18
135847	131884	124182	112595	097140	078152	056655	034281	014945	003754	16
133953	129632	121566	109631	093880	074703	053104	031150	012573	002545	14
132113	127451	119042	106784	090767	071439	049885	028290	010508	001621	12
130328	125342	116610	104053	087801	068354	046885	025691	008729	000949	10
122216	115837	105764	092045	075000	055411	034843	016071	003322	000000	00
1.22	1.50	1.86	2.33	3.00	4.00	5.67	9.00	19.00	∞	F/M
0.61	0.75	0.93	1.20	1.50	2.00	2.90	4.50	9.50	∞	F/K

Appendix 1 (*continued*)

YIELD TABLES FOR M/K = 0.50,

$M/K = 1.00$

E	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50
c										
98	000970	001938	002904	003869	004831	005791	006749	007704	008657	009606
96	001880	003754	005621	007481	009333	011177	013011	014835	016647	018447
94	002734	005454	008160	010849	013521	016174	018806	021416	024001	026559
92	003534	007043	010527	013982	017408	020800	024156	027473	030748	033976
90	004281	008525	012730	016892	021007	025071	029081	033031	036916	040730
88	004979	009906	014777	019587	024331	029004	033601	038113	042534	046855
86	005629	011189	016674	022077	027394	032615	037734	042742	047628	052381
84	006234	012379	018428	024373	030207	035920	041501	046941	052225	057341
82	006796	013481	020047	026484	032783	038932	044920	050731	056352	061764
80	007316	014498	021536	028419	035134	041669	048008	054135	060032	066680
78	007797	015435	022903	030186	037271	044143	050783	057173	063293	069117
76	008241	016297	024153	031795	039206	046369	053263	059866	066156	072104
74	008650	017086	025293	033254	040950	048361	055463	062234	068645	074668
72	009025	017807	026329	034571	042513	050131	057401	064296	070784	076835
70	009368	018463	027266	035754	043905	051694	059092	066070	072595	078630
68	009682	019059	028110	036812	045138	053061	060552	067575	074097	080079
66	009967	019597	028867	037751	046220	054246	061794	068829	075314	081205
64	010226	020082	029542	038579	047162	055259	062834	069849	076264	082033
62	010460	020516	030140	039303	047972	056112	063685	070651	076966	082584
60	010670	020902	030666	039930	048659	056817	064362	071252	077441	082880
58	010859	021244	031125	040467	049233	057383	064876	071666	077705	082943
56	011027	021545	031522	040920	049701	057823	065241	071910	077777	082792
54	011176	021808	031861	041295	050071	058144	065469	071996	077673	082447
52	011308	022035	032146	041599	050351	058358	065571	071939	077410	981927
50	011423	022230	032382	041836	050549	058474	065559	071753	077002	081250
48	011523	022394	032572	042014	050672	058499	065443	071450	076465	080433
46	011610	022531	032721	042136	050727	058444	065234	071042	075814	079492
44	011683	022642	032833	042208	050720	058315	064941	070541	075060	078443
42	011745	022731	032910	042236	050657	058121	064574	069958	074219	077301
40	011797	022798	032956	042223	050545	057870	064142	069304	073301	076080
38	011839	022847	032975	042173	050389	057567	063652	068588	072319	074793
36	011873	022879	032969	042092	050195	057221	063115	067820	071283	073454
34	011899	022896	032942	041984	049967	056837	062536	067009	070204	072073
32	011918	022900	032895	041851	049711	056420	061923	066164	069091	070661
30	011931	022892	032832	041697	049431	055978	061282	065291	067954	*069230
28	011939	022875	032756	041526	049131	055514	060621	064399	066801	*067788
26	011942	022849	032667	041341	048815	055034	059944	063493	065639	*066345
24	011942	022816	032569	041144	048487	054542	059256	062581	064475	*064908
22	011939	022778	032463	040938	048150	054042	058564	061668	063317	*063484
20	011933	022734	032351	040726	047807	053538	057870	060758	*062169	062080
18	011924	022687	032234	040510	047460	053033	057179	059857	*061037	060702
16	011914	022637	032115	040291	047113	052530	056495	058969	*059925	059354
14	011903	022586	031994	040072	046768	052032	055820	058096	*058837	058040
12	011891	022533	031872	039853	046425	051540	055156	057241	*057777	056765
10	011878	022480	031750	039637	046088	051058	054507	056408	*056746	055530
00	011814	022221	031170	038612	044505	048814	051514	*052597	052078	050000
F/M	0.0526	0.111	0.177	0.250	0.333	0.429	0.539	0.667	0.818	1.00
F/K	0.0530	0.110	0.180	0.250	0.330	0.430	0.540	0.670	0.820	1.00

For notes, see end of table.

1.00 AND 1.75[1]

$M/K = 1.00$

0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95	1.00	E
										c
010552	011494	012431	013364	014292	015214	016129	017036	017935	*018824	98
020234	022006	023761	025498	027215	028908	030576	032215	033821	*035389	96
029088	031584	034044	036463	038838	041164	043433	045641	047778	*049835	94
037152	040272	043330	046318	049230	052057	054789	057415	059921	*062295	92
044466	048116	051671	055122	058457	061664	064729	067635	070365	*072900	90
051066	055157	059116	062930	066583	070059	073338	076399	079220	*081777	88
056990	061439	065715	069798	073671	077312	080696	083799	086592	*089048	86
062273	067003	071513	075781	079783	083494	086885	089926	092585	*094833	84
066950	071889	076557	080929	084978	088673	091981	094868	097300	*099246	82
071056	076135	080891	085295	089314	092914	096059	098710	100834	*102400	80
074623	079781	084560	088928	092848	096282	099191	101536	103281	*104401	78
077684	082862	087605	091876	095634	098839	101450	103425	104733	*105354	76
080270	085415	090067	094185	097726	100645	102902	104455	105277	*105358	74
082411	087476	091987	095901	099174	101759	103613	104700	*104998	104509	72
084138	089077	093402	097069	100029	102236	103648	*104233	103978	102900	70
085478	090251	094351	097729	100338	102131	103068	*103123	102294	100618	68
086460	091031	094896	097925	100149	101497	*101932	101437	100022	097749	66
087110	091447	094992	097694	099506	*100384	100298	099239	097235	094372	64
087455	091528	094752	097076	098452	*098841	098219	096590	094000	090565	62
087518	091304	094184	096107	*097029	096914	095749	093550	090385	086400	60
087326	090802	093317	094823	*095276	094650	092938	090174	086450	081947	58
086900	090048	092182	*093257	093233	092089	089833	086516	082256	077271	56
086263	089068	090809	*091442	090935	089274	086481	082626	077858	072433	54
085437	087886	089224	*089410	088418	086244	082925	078554	073310	067492	52
084442	086526	*087454	087190	085714	083036	079207	074344	068662	062500	50
083298	085010	*085525	084810	082857	079684	075364	070040	063959	057508	48
082024	083360	*083460	082298	079874	076223	071435	065681	059247	052561	46
080637	*081595	081282	079679	076796	072684	067453	061306	054564	047703	44
079154	*079735	079012	076977	073649	069095	063451	056948	049948	042971	42
077592	*077797	076672	074214	070457	065486	059459	052641	045433	038400	40
*075965	075800	074280	071413	067245	061881	055504	048413	041049	034021	38
*074289	073759	071854	068592	064034	058304	051613	044292	036825	029860	36
*072576	071690	069411	065770	060844	054777	047808	040302	032785	025941	34
*070839	069605	066966	062965	057694	051319	044110	036465	028950	022282	32
069089	067518	064534	060191	054600	047950	040538	032800	025338	018900	30
067337	065441	062128	057464	051578	044684	037108	029322	021965	015805	28
065593	063385	059759	054795	048642	041537	033836	026046	018840	013006	26
063865	061360	057438	052197	045803	038519	030732	022982	015975	010506	24
062163	059373	055174	049678	043072	035642	027806	020138	013373	008305	22
060492	057434	052976	047249	040457	032914	025067	017522	011037	006400	20
058859	055548	050851	044915	037966	030341	022519	015134	008967	004782	18
057269	053721	048805	042682	035603	027928	020165	012977	007157	003441	16
055727	051958	046841	040556	033372	025678	018006	011046	005601	002360	14
054237	050262	044963	038538	031276	023590	016040	009338	004289	001521	12
052799	048635	043174	036630	029314	021664	014264	007845	003206	000900	10
046447	041558	035541	028694	021429	014286	007940	003147	000536	000000	00
1.22	1.50	1.86	2.33	3.00	4.00	5.67	9.00	19.00	∞	F/M
1.20	1.50	1.80	2.30	3.00	4.00	5.70	9.00	19.00	∞	F/K

Appendix 1 (*concluded*)

YIELD TABLES FOR M/K = 0.50,

$M/K = 1.75$

E	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50
c										
98	000051	000102	000153	000204	000255	000306	000356	000407	000457	000507
96	000165	000330	000495	000658	000822	000984	001146	001307	001468	001627
94	000323	000645	000965	001283	001600	001914	002227	002538	002846	003152
92	000514	001024	001531	002034	002533	003029	003520	004007	004489	004966
90	000729	001452	002168	002879	003582	004278	004967	005647	006319	006982
88	000692	001915	002859	003791	004713	005623	006521	007405	008276	009133
86	001209	002405	003586	004751	005899	007031	008144	009238	010311	011363
84	001466	002911	004336	005740	007120	008475	009805	011108	012383	013627
82	001727	003427	005100	006742	008354	009933	011478	012986	014456	015886
80	001991	003946	005866	007746	009587	011385	013138	014844	016501	018105
78	002254	004463	006626	008741	010804	012814	014767	016661	018493	020259
76	002514	004973	007375	009716	011994	014206	016349	018418	020411	022323
74	002769	005471	008104	010664	013147	015550	017869	020100	022238	024279
72	003258	005956	008811	011578	014255	016835	019316	021692	023958	026110
70	003258	006423	009489	012453	015310	018054	020681	023186	025562	027804
68	003489	006870	010136	013284	016306	019199	021956	024572	027039	029352
66	003711	007296	010749	014067	017241	020266	023136	025843	028383	030746
64	003921	007698	011326	014799	018109	021250	024215	026997	029588	031981
62	004119	008077	011865	015479	018909	022149	025192	028029	030652	033055
60	004306	008430	012365	016104	019639	022962	026064	028937	031574	033967
58	004480	008757	012825	016675	020298	023686	026831	029723	032354	034717
56	004641	009059	013245	017191	020887	024324	027493	030386	032993	035307
54	004790	009335	013626	017652	021405	024875	028052	030928	033494	035742
52	004927	009586	013966	018059	021854	025341	028511	031354	033862	036027
50	005051	009811	014268	018413	022235	025724	028871	031666	034100	036167
48	005164	010011	014532	018716	022551	026028	029137	031868	034215	036169
46	005264	010188	014760	018969	022804	026256	029313	031968	034212	036041
44	005354	010342	014953	019175	022997	026410	029410	031969	034100	035792
42	005432	010474	015112	019336	023134	026496	029414	031879	033886	035430
40	005501	010585	015240	019454	023217	026518	029350	031704	033577	034966
38	005560	010676	015338	019533	023250	026481	029217	031452	033182	034408
36	005609	010749	015408	019575	023238	026389	029021	031129	032710	033768
34	005651	010806	015453	019583	023183	026247	028768	030742	032170	033055
32	005684	010846	015475	019560	023091	026061	028465	030301	031570	032280
30	005710	010873	015476	019510	022965	025835	028117	029811	030919	*031453
28	005730	010887	015458	019435	022809	025575	027732	029280	030227	*030585
26	005745	010889	015424	019339	022627	025286	027314	028716	029500	*029684
24	005754	010882	015375	019224	022424	024973	026871	028126	028749	*028761
22	005758	010866	015313	019094	022203	024640	026408	027516	*027981	027826
20	005759	010843	015242	018951	021967	024292	025930	026894	*027203	026886
18	005757	010814	015162	018799	021721	023933	025443	026265	*026423	025950
16	005752	010780	015076	018639	021468	023568	024951	025636	*025648	025025
14	005745	010742	014986	018474	021210	023200	024460	*025010	024882	024118
12	005737	010702	014892	018306	020950	022833	023973	*024394	024133	023235
10	005727	010660	014796	018138	020692	022470	023493	*023791	023403	022381
00	005674	010448	014330	017331	019471	020779	*021293	021064	020156	018648
F/M	0.0526	0.111	0.177	0.250	0.333	0.429	0.539	0.667	0.818	1.00
F/K	0.0920	0.190	0.310	0.440	0.580	0.750	0.940	1.200	1.400	1.80

[1] The figure for the yield at the value of c giving the maximum yield for a given E is underlined.

1.00 AND 1.75[1]

$M/K = 1.75$

0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95	1.00	E
										c
000558	000608	000657	000707	000757	000806	000855	000904	000953	*001001	98
001786	001944	002101	002257	002411	002565	002717	002868	003018	*003165	96
003456	003757	004055	004350	004641	004929	005214	005494	005770	*006042	94
005437	005903	006362	006816	007262	007700	008131	008554	008967	*009371	92
007635	008278	008910	009530	010138	010733	011314	011880	012430	*012964	90
009974	010798	011606	012395	013164	013912	014639	015342	016021	*016673	88
012393	013397	014377	015329	016253	017146	018008	018835	019627	*020381	86
014840	016019	017162	018268	019334	020358	021338	022272	023157	*023157	84
017273	018615	019910	021155	022347	023485	024564	025582	026537	*027426	82
019655	021147	022578	023945	025244	026474	027630	028709	029708	*030625	80
021956	023581	025130	026599	027985	029283	030491	031604	032620	*033537	78
024151	025890	027537	029086	030535	031878	033111	034232	035238	*036125	76
026218	028052	029775	031382	032869	034231	035464	036565	037531	*038362	74
028142	030048	031825	033465	034966	036321	037527	038581	039481	*040228	72
029907	031865	033672	035322	036811	038133	039286	040266	041074	*041712	70
031505	033492	035306	036941	038393	039658	040732	041614	042305	*042809	68
032928	034921	036718	038316	039707	040890	041861	042620	043172	*043523	66
034170	036147	037906	039442	040750	041827	042672	043288	043680	*043860	64
035230	037170	038868	040320	041522	042472	043171	043624	*043839	043833	62
036107	037989	039606	040953	042028	042832	043366	043638	*043662	043457	60
036803	038606	040122	041345	042275	042913	043266	*043344	043164	042753	58
037321	039027	040422	041504	042271	042729	*042886	042758	042367	041745	56
037665	039257	040515	041438	042028	*042292	042243	041900	041292	040458	54
037842	039304	040410	041160	041559	*041618	041354	040791	039964	038921	52
037860	039177	040116	040681	*040879	040725	040239	039454	038410	037163	50
037726	038885	039646	*040015	040004	039630	038921	037913	036656	035215	48
037450	038439	039013	*039178	038951	038354	037420	036194	034733	033110	46
037042	037853	*038230	038185	037739	036918	035762	034324	032669	030881	44
036512	037136	*037311	037053	036386	035343	033971	032329	030495	028559	42
035873	*036304	036273	035799	034911	033651	032070	030238	028240	026178	40
035134	*035369	035129	034440	033336	031863	030084	028076	025935	023770	38
034308	*034344	033896	032994	031678	030003	028038	025871	023607	021366	36
*033408	033244	032589	031478	029959	028092	025957	023650	021286	018995	34
*032444	032082	031224	029910	028196	026151	023862	021437	018999	016686	32
031429	030871	029815	028307	026410	024201	021778	019256	016770	014464	30
030374	029625	028378	026686	024618	022262	019725	017131	014624	012354	28
029291	028357	026927	025061	022839	020354	017723	015083	012583	010377	26
028191	027078	025475	023450	021087	018493	015793	013131	010666	008552	24
027084	025801	024036	021864	019380	016696	013950	011292	008889	006893	22
025980	024536	022622	020319	017730	014979	012209	009582	007267	005414	20
024887	023294	021243	018825	016151	013353	010584	008013	005811	004121	18
023816	022084	019910	017393	014653	011830	009086	006595	004528	003019	16
022772	020914	018632	016033	013245	010418	007722	005333	003422	002107	14
021762	019790	017415	014751	011935	009126	006498	004232	002494	001382	12
020792	018719	016265	013553	010728	007955	005416	003292	001739	000832	10
016639	014246	011607	008883	006250	003898	002009	000730	000113	000000	00
1.22	1.50	1.86	2.33	3.00	4.00	5.67	9.00	19.00	∞	F/M
2.10	2.60	3.20	4.10	5.30	7.00	9.90	16.00	33.00	∞	F/K

[1] The maximum yield for a given value of c is indicated with an asterisk.

Appendix 2

TABLES OF e^{-x}

THE EXPONENTIAL e^{-x}

For values of x from .0000 to .0999

x	0	.001	.002	.003	.004	.005	.006	.007	.008	.009
.00	1.000	.9990	.9980	.9970	9960	.9950	.9940	.9930	.9920	.9910
.01	.9900	.9891	.9881	.9871	.9861	.9851	9841	.9831	.9822	.9812
.02	.9802	.9792	.9782	.9773	.9763	.9753	.9743	.9734	9724	.9714
.03	.9704	9695	.9685	.9675	.9666	.9656	9646	.9637	9627	.9618
.04	.9608	.9598	.9589	.9579	.9570	.9560	.9550	.9541	9531	.9522
.05	.9512	9502	.9493	.9484	9474	9465	.9455	.9446	.9436	.9427
.06	.9418	.9408	.9399	.9389	.9380	.9371	.9361	.9352	.9343	.9333
.07	.9324	.9315	.9305	.9296	.9287	.9277	.9268	.9259	.9250	.9240
.08	.9231	.9222	.9213	.9204	.9194	.9185	.9176	.9167	.9158	.9148
.09	.9139	.9130	.9121	.9112	.9103	.9094	.9085	9076	.9066	.9057

Subtract differences

.0001	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	8
1	2	3	4	5	6	7	7	8
1	2	3	4	5	6	6	7	8

For values of x from .100 to 2.999

x	0	.01	.02	.03	.04	.05	.06	.07	.08	.09
.1	.9048	.8958	.8869	.8781	.8694	.8607	.8521	.8437	.8353	.8270
.2	8187	.8106	.8025	.7945	.7866	.7788	.7711	.7634	.7558	.7483
.3	.7408	.7334	.7261	.7189	.7118	.7047	.6977	.6907	.6839	.6771
.4	.6703	.6637	.6570	.6505	.6440	.6376	6313	.6250	.6188	.6126
.5	.6065	.6005	.5945	.5886	.5827	.5769	.5712	.5655	.5599	.5543
.6	.5488	.5434	.5379	.5326	.5273	.5220	.5169	.5117	.5066	.5016
.7	.4966	.4916	.4868	.4819	.4771	.4724	.4677	.4630	.4584	.4538
.8	.4493	.4449	.4404	.4360	.4317	.4274	.4232	.4190	.4148	.4107
.9	.4066	.4025	.3985	.3946	.3906	.3867	3829	.3791	.3753	.3716
1.0	.3679	.3642	.3606	.3570	.3535	.3499	.3465	.3430	.3396	.3362
1.1	.3329	.3296	.3263	.3230	.3198	.3166	.3135	.3104	.3073	.3042
1.2	.3012	.2982	.2952	.2923	.2894	.2865	.2837	.2808	.2780	.2753
1.3	.2725	.2698	.2671	.2645	.2618	.2592	.2567	.2541	.2516	.2491
1.4	.2466	.2441	.2417	.2393	.2369	.2346	.2322	.2299	.2276	.2254
1.5	.2231	.2209	.2187	.2165	.2144	2122	.2101	.2080	.2060	.2039
1.6	.2019	.1999	.1979	.1959	.1940	.1920	.1901	.1882	.1864	1845
1.7	1827	.1809	.1791	.1773	.1755	.1738	.1720	.1703	.1686	1670
1.8	.1653	.1637	.1620	.1604	.1588	.1572	.1557	1541	.1526	.1511
1.9	.1496	.1481	.1466	.1451	.1437	.1423	.1409	.1395	.1381	.1367
2.0	.1353	.1340	.1327	.1313	.1300	.1287	.1275	.1262	.1249	.1237
2.1	.1225	.1212	.1200	.1188	.1177	.1165	.1153	.1142	.1130	.1119
2.2	.1108	.1097	.1086	.1075	.1065	.1054	.1044	.1033	.1023	.1013
2.3	.1003	.0993	.0983	.0973	.0963	.0954	.0944	.0935	.0926	.0916
2.4	.0907	.0898	.0889	.0880	.0872	.0863	.0854	.0846	.0837	.0829
2.5	.0821	.0813	.0805	.0797	.0789	.0781	.0773	.0765	.0758	.0750
2.6	.0743	.0735	.0728	.0721	.0714	.0707	.0699	.0693	.0686	.0679
2.7	.0672	.0665	.0659	.0652	.0646	.0639	.0633	.0627	.0620	.0614
2.8	.0608	.0602	.0596	.0590	.0584	.0578	.0573	.0567	.0561	.0556
2.9	.0550	.0545	.0539	.0534	.0529	.0523	.0518	.0513	.0508	.0503

Subtract differences

.001	2	3	4	5	6	7	8	9
9	17	26	34	43	52	60	69	77
8	16	23	31	39	47	55	62	70
7	14	21	28	35	42	49	56	63
6	13	19	26	32	38	45	51	57
6	12	17	23	29	35	40	46	52
5	10	16	21	26	31	37	42	47
5	9	14	19	24	28	33	38	43
4	9	13	17	21	26	30	34	38
4	8	12	15	19	23	27	31	35
4	7	11	14	18	21	25	28	32
3	6	9	13	16	19	22	25	29
3	6	9	11	14	17	20	23	26
3	5	8	10	13	16	18	21	23
2	5	7	9	12	14	16	19	21
2	4	6	8	11	13	15	17	19
2	4	6	8	10	12	13	15	17
2	3	5	7	9	10	12	14	16
2	3	5	6	8	9	11	13	14
1	3	4	6	7	9	10	11	13
1	3	4	5	6	8	9	10	12
1	2	4	5	6	7	8	9	11
1	2	3	4	5	6	7	8	9
1	2	3	4	5	6	7	8	9
1	2	3	3	4	5	6	7	8
1	2	2	3	4	5	5	6	7
1	1	2	3	4	4	5	6	6
1	1	2	3	3	4	4	5	6
1	1	2	2	3	3	4	5	5
1	1	2	2	3	3	4	4	5

For values of x from 3.0 to 8.9

x	0	.1	.2	.3	.4	.5	.6	.7	.8	.9
3	.0498	.0450	.0408	.0368	0334	.0302	.0273	.0247	.0224	.0202
4	.0183	.0166	.0150	.0136	.0123	.0111	.0101	.0091	.0082	.0074
5	.0067	.0061	.0055	.0050	.0045	.0041	.0037	.0033	.0030	.0027
6	.0025	.0022	.0020	.0018	.0017	.0015	.0014	.0012	.0011	.0010
7	.0009	.0008	.0007	.0007	.0006	.0006	.0005	.0005	.0004	.0004
8	.0003	.0003	.0003	.0002	.0002	.0002	.0002	.0002	.0002	.0001

Subtract differences

Mean differences no longer sufficiently accurate

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